AN ABSTRACT OF THE THESIS OF

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Title: Quaking Aspen Persistence in Three Oregon Landscapes.

Abstract approved:

William J. Ripple

Quaking aspen (*Populus tremuloides*) is an important tree species in the western United States and there has been much concern about its persistence. In this thesis, I report on aspen in a portion of its range that has not been previously evaluated: the eastern and western slopes of the Central Oregon Cascades and the Willamette Valley. My primary research objectives for each of the three landscapes were to: (1) assess aspen overstory recruitment across time; (2) assess the condition of aspen sprouts; (3) identify environmental and biological stressors to the aspen overstory and understory; and (4) test the aspen overstory, recent recruitment, and sprouts for correlations to ungulate herbivory and conifer encroachment. In addition, on the eastern slope of the Cascades, I tested the efficacy of piles of coarse woody debris (CWD) or jackstraw as an herbivore deterrent.

On the east side of the Cascade Mountains, aspen stands were small (≤ 0.6 ha) and found in a dense conifer matrix. Small stands are expected to recruit overstory across time and expand with disturbance events. Aspen stands on the east side showed a steady decline in overstory recruitment that coincided with increase in conifer

encroachment and ungulate herbivory. Aspen stands with conifer mortality attributable to mountain pine beetle (*Dendroctonus ponderosae),* and subsequent release of overstory competition and formation of jackstraw, recruited overstory trees at expected levels. More than 75% of all recently recruited trees (< 20 years) were behind jackstraw. Diseased sprouts protected from herbivores recruited into the overstory. My results suggest that aspen sprouts increase in height when released from herbivory and increase in density when released from conifer shading and competition. Accordingly, I suggest that the mountain pine beetle has a powerful ecological effect that can help aspen recruit at the stand level and persist at the landscape level via: (1) removal of conifer shading and resource competition; (2) creation of snags, and subsequent increase in jackstraw; and (3) the ensuing increase in sprout density and heights, which leads to overstory recruitment.

Results in the two western Oregon landscapes show aspen stands are small (< 0.1 ha), rare, and in decline. Stand origins are unknown and could be genetically linked to stands on the east Cascades or to the north. While most aspen stems dated back to the early to mid 1900s, one stem originated in the mid 1800s. I classified 16 aspen stands from these two landscapes into 6 stand types: Snowfield, Upland Aspen/Conifer, Meadow Fringe, Lithic/Boulder, Pasture Valley, and Riparian Valley. One stand type was found increasing, 3 types were decreasing, and 2 types were at risk of loss. I found aspen sprouts were suppressed by herbivory, disease, and conifer encroachment. Some stand types showed aspen overstory at risk from conifer encroachment.

Aspen is on the fringe of its range on the east and west slopes of the Oregon Cascades and in the Willamette Valley. A scientific understanding of aspen in these three landscapes may help the persistence of this species in the face of climate change.

Quaking Aspen Persistence in Three Oregon Landscapes

by

S Trent Seager

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

S Trent Seager, Author

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CONTRIBUTION OF AUTHORS

William J. Ripple assisted with study design, data analysis, and writing of Chapters 2 and 3.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1 – INTRODUCTION

Aspen (*Populus* spp.) is the most widespread tree species globally (Worrell, 1995) and in North America (Little, 1971). In the Intermountain Region of the western United States, quaking aspen (*Populus tremuloides*) is the only upland deciduous tree (Debyle and Winokur, 1985). In Oregon, aspen is considered a species of the dry Northern Basin and Range or Blue Mountains ecoregions (Miller and Rose, 1995; ODFW, 2006). However, aspen occurs in many parts of the state, including the wetter, western side of Oregon (Little, 1971). Aspen is one of few deciduous trees on the east slope of the Oregon Cascade Mountains, and is considered an important part of that region's dry forest restoration (Johnson and Franklin, 2009).

Although widely distributed, aspen makes up only a small portion of forested land in the US Intermountain West. As such, aspen ecosystems provide a disproportionate amount of plant and wildlife habitat in addition to overall biodiversity in an otherwise dry region (Mueggler, 1985; White *et al.*, 1998). This biodiversity is documented across multiple food web levels and taxa including: bryophytes, lichens, and fungi (Crites and Dale, 1998), arthropods (Bailey and Whitham, 2002), avifauna (Flack, 1976; Dobkin, 1995; Griffis-Kyle and Beier, 2003), small mammals (Oaten and Larsen, 2009), and large mammals (see Debyle, 1985b; Fisher and Wilkinson, 2005 for a reviews). The recent decline of aspen in some parts of the western US has generated much concern about this species' persistence (Romme *et al.*, 1995; Kay, 1997b; Ripple and Larsen, 2000). Aspen are sensitive to drought (Hogg *et al.*, 2008) and biophysical settings (Brown *et al.*, 2006). Some researchers have linked recent episodes of sudden aspen decline to climate change (Worrall *et al.*, 2008). Other factors identified as playing a role in aspen decline include herbivory, pest and disease outbreak, conifer encroachment, and fire and disturbance regimes (Romme *et al.*, 1995; Bartos, 2001; Kulakowski *et al.*, 2004; Ripple and Beschta, 2007; Worrall *et al.*, 2008).

Aspen is a clonal species that reproduces through root sprouting in addition to seeding under the right conditions, such as post-fire (Schier *et al.*, 1985; Romme *et al.*, 2005). A shade intolerant species, aspen is susceptible to conifer encroachment. Aspen sprouts require the high soil temperatures and levels of solar radiation that come from open areas around the stand or areas where disturbance has opened up the overstory (Schier *et al.*, 1985; Carlson and Groot, 1997).

The diversity of landscapes where aspen occur allows for a variety of ecological factors that lead to aspen stand persistence or decline, emphasizing the need for research of the specific drivers for each geographic location (Kashian *et al.*, 2007). Land managers working to restore aspen ecosystems as part of dry forest restoration must prepare for possible new climactic stressors on the aspen (Rehfeldt *et al.*, 2009). Decreasing current pressures on aspen stands, specifically herbivory and conifer shading, can increase aspen stand size and vigor (White *et al.*, 1998; Bartos, 2001), making them less susceptible to larger climactic patterns (Gitlin *et al.*, 2006).

Few studies have looked at the current extent and conservation status of aspen in Oregon. Aspen research has focused on the dry Northern Basin and Range and

Blue Mountain ecoregions of eastern Oregon (Miller and Rose, 1995; Shirley and Erickson, 2001; Wall *et al.*, 2001; Bates *et al.*, 2006).

In this thesis, I examine aspen persistence in three Oregon landscapes: (1) eastern slope of the Oregon Cascades; (2) western slope of the Oregon Cascades; and (3) the Willamette Valley. Aspen is on the fringe of its range in these landscapes, and the species has not been studied here. Chapter 2 considers the effects of herbivory, conifer encroachment, and coarse woody debris on aspen persistence on the east side of the central Oregon Cascades. This fire-dependent landscape has been under active and passive fire suppression for over a century and experienced decades of an irruptive deer population. Chapter 3 provides a study of aspen in western Oregon, identifying stand types and stressors in a region with three times the average annual precipitation normally associated with aspen.

This work provides new information about aspen in Oregon and provides valuable information to land managers that prioritize aspen restoration. In addition, this thesis offers scientific findings and suggestions applicable to aspen ecosystems in general, and therefore is relevant to scientists and managers at a much broader geographic area.

LITERATURE CITED

Bailey, J.K., Whitham, T.G., 2002. Interactions among Fire, Aspen, and Elk Affect Insect Diversity: Reversal of a Community Response. Ecology 83, 1701-1712.

Bartos, D.L., 2001. Landscape dynamics of aspen and conifer forests.

Bates, J.D., Miller, R.F., Davies, K.W., 2006. Restoration of Quaking Aspen Woodlands Invaded by Western Juniper. Rangeland Ecology and Management 59, 88-97.

Brown, K., Hansen, A., Keane, R., Graumlich, L., 2006. Complex interactions shaping aspen dynamics in the Greater Yellowstone Ecosystem. Landsc Ecol 21, 933-951.

Carlson, D.W., Groot, A., 1997. Microclimate of clear-cut, forest interior, and small openings in trembling aspen forest. Agricultural and Forest Meteorology 87, 313-329.

Crites, S., Dale, M.R.T., 1998. Diversity and abundance of bryophytes, lichens and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. Can J Bot 76, 641–651.

Debyle, N.V., 1985. Wildlife *in* Aspen: Ecology and management in the western United States. General Technical Report RM-119., Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, 135-152.

Debyle, N.V., Winokur, R.P., 1985. Aspen: Ecology and management in the western United States. General Technical Report RM-119., Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, 283p.

Dobkin, D.S., Rich, A.C., Pretare, J.A. and Pyle, W.H., 1995. Nest–site relationships among cavity-nesting birds of the riparian and snowpocket aspen woodlands in the northwestern Great Basin. Condor 97, 694–707.

Fisher, J.T., Wilkinson, L., 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mammal Rev 35, 51-81.

Flack, D.J.A., 1976. Bird populations of aspen forests in western North America. Ornithol Monogr 19, 1-97.

Gitlin, A.R., Sthultz, C.M., Bowker, M.A., Stumpf, S., Paxton, K.L., Kennedy, K., Muñoz, A., Bailey, J.K., Whitham, T.G., 2006. Mortality Gradients within and among Dominant Plant Populations as Barometers of Ecosystem Change During Extreme Drought. Conserv Biol 20, 1477-1486.

Griffis-Kyle, K.L., Beier, P., 2003. Small isolated aspen stands enrich bird communities in southwestern ponderosa pine forests. Biol Conserv 110, 375-385.

Hogg, E.H.T.e.d., Brandt, J.P., Michaelian, M., 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Can J For Res 38, 1373-1384.

Johnson, N.K., Franklin, J.F., 2009. Restoration of Federal Forests in the Pacific Northwest: Strategies and Management Implications. Special report to Senator Wyden and Congressman DeFazio., 120 pp.

Kashian, D.M., Romme, W.H., Regan, C.M., 2007. Reconciling Divergent Interpretations of Quaking Aspen Decline on the Northern Colorado Front Range. Ecol Appl 17, 1296-1311.

Kay, C.E., 1997. Is Aspen Doomed? J For 95, 4-11.

Kulakowski, D., Veblen, T.T., Drinkwater, S., 2004. The Persistence of Quaking Aspen (Populus Tremuloides) in the Grand Mesa Area, Colorado. Ecol Appl 14, 1603-1614.

Little, E.L., Jr., 1971. Conifers and important hardwoods. Volume I. Atlas of United States trees. Forest Service Miscellaneous Publication Number 1146, Washington D.C., USA.

Miller, R.E., Rose, J.A., 1995. Historic Expansion of Juniperus-Occidentalis (Western Juniper) in Southeastern Oregon. Great Basin Nat 55, 37-45.

Mueggler, W.F., 1985. Vegetation associations. Pages 45–55 in N. V. DeByle and R. P. Winokur, editors. Aspen: ecology and management in the western United States. General Technical Report RM-119. United States Department of Agriculture Forest Service, Fort Collins, Colorado, USA.

Oaten, D.K., Larsen, K.W., 2009. Aspen Stands as Small Mammal "Hotspots" Within Dry Forest Ecosystems of British Columbia. Northwest Sci 82, 276-285.

ODFW, 2006. Aspen Woodlands, in Oregon Conservation Strategy. Oregon Department of Fish and Wildlife, Salem, Oregon. , 259-260.

Rehfeldt, G.E., Ferguson, D.E., Crookston, N.L., 2009. Aspen, climate, and sudden decline in western USA. For Ecol Manage 258, 2353-2364.

Ripple, W.J., Beschta, R.L., 2007. Restoring Yellowstone's aspen with wolves. Biol Conserv 138, 514-519.

Ripple, W.J., Larsen, E.J., 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. Biol Conserv 95, 361-370.

Romme, W.H., Turner, M.G., Tuskan, G.A., Reed, R.A., 2005. Establishment, Persistence, and Growth of Aspen (Populus tremuloides) Seedlings in Yellowstone National Park. Ecology 86, 404-418.

Romme, W.H., Turner, M.G., Wallace, L.L., Walker, J.S., 1995. Aspen, Elk, and Fire in Northern Yellowstone Park. Ecology 76, 2097-2106.

Schier, G.A., Jones, J.R., Winokur, R.P., 1985. Vegetative regeneration. In: N. V. DeByle and R. P. Winokur, eds. Aspen: ecology and management in the western United States. USDA, For. Serv. Rocky Mountain Forest and Range Experiment Station. Fort Collins, CO. Gen. Tech. Rep RM-119: 20–33.

Shirley, D.M., Erickson, V., 2001. Aspen restoration in the Blue Mountains of Northeast Oregon. Pages 101-115 in Shepperd et al., compilers. Sustaining aspen in western landscapes: Symposium Proceedings. USDA Forest Service Rocky Mountain Research Station, RMRSP- 18, Grand Junction, Colorado.

Wall, T.G., Miller, R.F., Svejcar, T.J., 2001. Juniper encroachment into aspen in the Northwest Great Basin. J Range Manage 54, 691-698.

White, C.A., Olmsted, C.E., Kay, C.E., 1998. Aspen, Elk, and Fire in the Rocky Mountain National Parks of North America. Wildl Soc Bull 26, 449-462.

Worrall, J.J., Egeland, L., Eager, T., Mask, R.A., Johnson, E.W., Kemp, P.A., Shepperd, W.D., 2008. Rapid mortality of Populus tremuloides in southwestern Colorado, USA. For Ecol Manage 255, 686-696.

Worrell, R., 1995. European aspen (Populus tremula L.): a review with particular reference to Scotland I. Distribution, ecology and genetic variation. Forestry 68, 93-105.

CHAPTER 2 – THE EFFECTS OF HERBIVORY, CONIFER ENCROACHMENT, AND COARSE WOODY DEBRIS ON ASPEN PERSISTENCE IN THE CENTRAL OREGON CASCADES

ABSTRACT

Ungulate herbivory and conifer shading have been shown to have negative effects on quaking aspen (*Populus tremuloides* Michx.) sprouts and stem recruitment in some parts of the western United States. We evaluated the effects of mule deer (*Odocoileus hemionus hemionus*), elk (*Cervus elaphus*), and livestock herbivory and conifer encroachment on aspen stands on the eastern slope of the Central Oregon Cascades. Within our study area, we sampled from all known aspen stands, measured and aged all the aspen stems using an age-diameter relationship, and established belt transects in each stand to sample aspen sprouts for effects from herbivory, disease, and conifer encroachment. Aspen stands showed a steady decline in overstory recruitment from the 1960s to the 1990s when compared to a refugium. This decline occurred after 30-years of an irruptive mule deer population and 50-years of active fire suppression and concurrent increase in coniferous trees. The exception to the overstory recruitment decline occurred in aspen stands with conifer mortality attributable to mountain pine beetle (*Dendroctonus ponderosae)*. The beetle-kill allowed a release of overstory competition and subsequent formation of coarse woody debris piles (jackstraw) that acted as an herbivore barrier. More than 75% of all stems that had recently recruited into the overstory in our study area (< 20 years) occurred behind jackstraw. Stands with jackstraw were characterized by higher levels of stem recruitment, fewer sprouts browsed, and taller sprouts than those without jackstraw.

Similar to fences, sprouts behind jackstraw were taller than those accessible to herbivores. We found disease alone did not suppress sprouts. Diseased sprouts behind herbivore barriers recruited into the overstory. Conifer shading decreased aspen sprout density. Our results suggest that aspen sprouts increase in height when released from herbivory and increase in density when released from conifer shading and competition. Accordingly, we suggest that the mountain pine beetle may be providing an ecosystem service by increasing aspen persistence via: (1) removal of conifer shading and resource competition; (2) creation of snags, and subsequent increase in coarse woody debris piles which acts as an herbivore barrier; and (3) the ensuing increase in sprout density and heights, which leads to overstory recruitment.

INTRODUCTION

Although quaking aspen (*Populus tremuloides* Michx.) is the most widely distributed tree species in North America (Little, 1971), it covers less than 10% of the forested landscape in the Intermountain West (Debyle and Winokur, 1985). In this region, aspen stands are considered “biodiversity hotspots” with more plant, insect, bird and mammal species than other forest types in the (Flack, 1976; Debyle, 1985b; Mueggler, 1985; Chong *et al.*, 2001; Bailey and Whitham, 2002; Oaten and Larsen, 2009). The recent decline of aspen in some parts of the western United States has generated much concern about this species’ persistence (Romme *et al.*, 1995; Kay, 1997b; Ripple and Larsen, 2000). Aspen are sensitive to drought (Hogg *et al.*, 2008) and biophysical settings (Brown *et al.*, 2006). Some researchers have linked recent episodes of aspen dieback (termed sudden aspen decline) to climate change (Worrall *et al.*, 2008). Other factors identified as playing a role in aspen decline include herbivory, pest and disease outbreak, conifer encroachment, and fire and disturbance regimes (Romme *et al.*, 1995; Bartos, 2001; Kulakowski *et al.*, 2004; Ripple and Beschta, 2007; Worrall *et al.,* 2008).

Aspen is a clonal species that reproduces through root sprouting in addition to seeding under the right conditions, such as post-fire (Schier *et al.*, 1985; Romme *et al.*, 2005). A shade intolerant species, aspen is susceptible to conifer encroachment. Aspen sprouts require high soil temperatures and levels of solar radiation that come from open areas around the stand or areas where disturbance has opened up the overstory (Schier *et al.*, 1985; Carlson and Groot, 1997). Stable aspen stands are able to recruit stems into the overstory and persist across time. Seral aspen stands are encroached by conifers or over-browsed by ungulates, and require disturbance or protection (e.g., fencing) to persist (Mueggler, 1985; Bartos, 2001). Small aspen stands tend to be composed of trees that are uneven age (Betters and Woods, 1981). They recruit stems through small gaps in the overstory (Cumming *et al.*, 2000), and persist until a disturbance such as fire allows stand expansion (Kay, 1997a).

Aspen sprouts are a preferred browse of wild and domestic ungulates (see Debyle, 1985a for a review). *Refugia*, or areas protected from herbivory, can provide important baseline data on expected plant diversity and occurrence when compared to areas with high levels of domestic and wild ungulates (see Milchunas and Noy-Meir, 2002; Ripple and Beschta, 2005 for reviews). Studies from different parts of the western US have reported coarse woody debris (CWD) acting as a barrier to ungulates and protecting aspen sprouts. In Arizona, Reynolds (1969) counted 30-50% fewer deer, elk, and cow dropping groups and found higher amounts of aspen sprouts and herbaceous understory in aspen stands with felled trees than those without. In the Black Hills of South Dakota, researchers found that excluding cattle (but not wild ungulates) with slash piles was as effective as fencing to maintain aspen regeneration 19 years later (Rumble *et al.*, 1996). Another study in the Black Hills tested different barrier types and found hinged trees and slash piles were successful in protecting aspen sprouts for the first year from livestock, deer, and elk (Kota, 2005). Studies in Yellowstone National Park found that post-fire snags can form CWD piles, that are barriers to ungulates and protect aspen sprouts (Ripple and Larsen, 2001; Romme *et al.*, 2005) though not necessarily on the landscape scale (Forester *et al.*, 2007). To our knowledge, no one has reported on how CWD created by beetle-kill can act as a barrier to ungulates, thereby protecting aspen sprouts.

The diversity of landscapes where aspen occurs allows for a variety of ecological factors that lead to aspen stand persistence or decline, emphasizing the need to research the specific drivers for each geographic location (Kashian *et al.*, 2007). Land managers working to restore aspen ecosystems as part of dry forest restoration must prepare for possible new climactic stressors on the aspen (Rehfeldt *et al.*, 2009). Decreasing current pressures on aspen stands, specifically herbivory and conifer shading, can increase aspen stand size and vigor (White *et al.*, 1998; Bartos, 2001), making them less susceptible to long-term climactic patterns (Gitlin *et al.*, 2006).

Few studies have looked at the current extent and conservation status of aspen in Oregon. Studies conducted in the dry Great Basin regions of eastern Oregon found aspen declining due to competition with western juniper (*Juniper occidentalis*), and concluded that since herbivory is minimal, restoration of aspen stands should focus on conifer removal and reintroducing fire (Miller and Rose, 1995; Wall *et al.*, 2001; Bates *et al.*, 2006). In contrast, a study in the Blue Mountains of eastern Oregon found that in addition to conifer removal and livestock exclusion, winter elk exclusion was necessary for aspen recruitment (Shirley and Erickson, 2001). One of few deciduous trees on the east slope of the Oregon Cascade Mountains, aspen is critical wildlife habitat (ODFW, 2006) and thus an important part of dry forest restoration (Johnson and Franklin, 2009).

The objectives of this study were to: (1) assess aspen overstory recruitment across time; (2) assess the condition of aspen sprouts on the eastern slope of the Central Oregon Cascade Mountains; (3) test the efficacy of CWD piles in protecting aspen sprouts from herbivory; and (4) test the overstory, recent recruitment, and sprouts for correlations to ungulate herbivory and conifer encroachment.

Study Area

Our ~ 70,000 ha study area lies on the east slope of the Central Oregon Cascade Mountains on the Chemult Ranger District of the Fremont-Winema National Forest, approximately 100 km south of Bend, Oregon (Figure 2.1). In our study area, aspen manifests as discrete, small stands (≤ 0.6 ha) embedded in a conifer matrix, including mature stands of ponderosa pine (*Pinus ponderosa*). This is different from the intermountain west (e.g., Colorado, Wyoming) where aspen can manifest as *parklands* between conifers and grasslands, or extensive stands on mountainsides, both typically > 30 ha in size (Kulakowski *et al.*, 2004).

Our study area featured an herbivore suite of deer-elk-livestock. The Chemult Ranger District had separate cattle (*Bos* spp.) and sheep (*Ovis aries*) grazing allotments, both of which included aspen stands. Domestic livestock were in our study area from July through September. Deer and elk do not overwinter in our study area, leaving for their winter ranges between October and November (Zalunardo, 1965; Verts and Carraway, 1998). We therefore operated under the assumption that in our study area aspen sprouts were only browsed in summer and fall.

The Crescent Ranger District (Deschutes National Forest), which borders our study area to the north, discontinued livestock grazing in the late 1980s, leaving only deer and elk as large herbivores. Additionally, this district managed many of its aspen stands via conifer thinning and fencing. We included 3 aspen stands from this district in our study for comparison purposes: of which 2 were treated for conifer removal and partially fenced (one in 1999, see Figure 2.5; and one in 2001), and 1 stand located in a campground used by people between spring snowmelt and late fall snowfall. We classified this campground stand as a *refugium* from herbivory, with little to no wild ungulate use over time because of human presence. We used this site for comparison against herbivore-accessible aspen stands across time. The managers removed conifers and fenced part of the campground aspen stand in 2004. We note these comparison stands separately in our analysis and results.

Elevation of aspen stands in our study area ranged from 1380 m to 1640 m. This area receives an average annual precipitation of 62 cm, most of it falling as snow. Summer precipitation is ~ 8% of total annual precipitation. Plant associations included ponderosa pine; lodgepole pine (*P. contorta*); mixed conifer including ponderosa pine, lodgepole pine, western white pine (*P. monticola*), and Engleman's spruce (*Picea englemanii*). White fir (*Abies concolor*) and Shasta red fir (*A. magnifica*) occurred at higher elevations, but the ranger district did not identify any aspen stands in these vegetation types.

Top predators, the gray wolf (*Canis lupus)* and the grizzly bear (*Urus arctos*), were extirpated from this region by 1930, though they were likely reduced to low numbers by 1910 (Bailey, 1936), and therefore had little effect on ungulate populations after that time. Rocky mountain elk (*Cervus elaphus nelsoni*) and Roosevelt elk (*Cervus elaphus roosevelti*) occur in our study area, but were nearly extirpated by 1910 (Bailey, 1936; ODFW, 2003a). Starting in the late 1940s, elk were reintroduced throughout the Oregon Cascades (Harper, 1985) and the current population for our study area is estimated at 1,000 (ODFW, 2003a). By comparison, mule deer populations *irrupted* in south-central Oregon from the 1930s to the 1960s in the absence of top predators and with coyote control programs (Salwasser, 1979). By the late 1970s, the lack of available forage and the end of predator suppression programs heavily impacted mule deer, causing their populations to drop by 60% and remain there today (Salwasser, 1979; Peek *et al.*, 2002; ODFW, 2003b). Since 1990 the Oregon Division of Fish and Wildlife (ODFW) have managed the mule deer herd in the Fort Rock Wildlife Management Unit, which comprises our study area, at a level of ~ 12,000 individuals or ~ 2.4 deer/km^2 (2003b).

Pre-1920s mean fire return interval (MFRI) estimates in dry-mixed conifer forests in the Central Oregon Cascades are 6-8 years (Bork, 1985). Currently, fire return intervals are greater than 70 years due to fire suppression, changing land use practices in grazing and forest management, and changing demographics (Agee, 1993; Hessburg and Agee, 2003). In the absence of fire, lodgepole pine trees increase in density and have corresponding stress and susceptibility to the mountain pine beetle (*Dendroctonus ponderosae)*, a native insect to western North American forests (Larsson *et al.*, 1983). In Central Oregon, a mountain pine beetle outbreak began in late 1970s, peaked in the mid 1980s and continued into the 1990s (Mitchell and Preisler, 1998; Williams and Liebhold, 2002). Lodgepole pine in the area were particularly affected and experienced heavy mortality, creating large amounts of snags that fell within a decade (Mitchell and Preisler, 1998).

METHODS

Field Methods

We defined an aspen *stem* as a tree ≥ 2.5 m in height. This height is considered above the height to which deer and elk are able to browse young trees (Baker *et al.*, 1997). Aspen *sprouts* were clonal root suckers or seedlings < 2.5 cm in height. We defined an aspen *stand* as a group of stems with an overstory of at least five stems > 8 cm diameter at breast height (DBH) located ≥ 20 m from other aspen stems. We defined the *stand area* as the polygon formed by all the aspen stems (overstory core) and the outermost sprouts (regeneration periphery), which we standardized to 10 m out from the overstory core (Keyser *et al.*, 2005). Aspen stands were excluded from our study if they had burned in the last 30 years, had beaver damage (recent or historic), or lay along a railroad. These elements create confounding factors that influence aspen stem recruitment across time. We also excluded stands that contained more than 500 aspen stems, as there were few in our study area and this would have created a scale issue when compared to small stands. Starting at the north end of the Chemult Ranger District, we visited each aspen stand identified by the USFS to see if it met our criteria for inclusion in our study.

To create an age-diameter relationship for aspen, we cored a subset of 35 aspen stems ≥ 6 cm DBH. To represent the range of the DBH size classes in the study area, we cored at least one tree in each stand that fit in a needed size class and did not show signs of fungal or core rot, selecting these trees haphazardly. We cored the trees at a height of 1.4 m, then dried, mounted, and sanded the cores using standard dendrochronological procedures (Stokes and Smiley, 1968) and counted the annual rings using a Unislide "TA" tree-ring measuring system (Velmex, Bloomfield, New York, USA). If tree cores did not intersect the center pith, we estimated the number of missing rings using a clear sheet matching the curvature of the innermost ring in the sample (Applequist, 1958). If the cores were estimated to be missing > 10 center rings, they were not included in our analysis. Additionally, we cut down at breast height a subset of 32 stems ≤ 5 cm DBH. This allowed us to age trees too small to core. We quantified an aspen age-diameter relationship from the 35 complete cores and 32 sectioned stems. Additional years were added for the average amount of time it took 35 sprouts to reach breast height.

All aspen stems and coniferous trees ≥ 2.5 m in height within the stand were measured with a Biltmore stick. As a metric to characterize aspen stand conservation status (ability to persist over time) Kay (1985) developed an aspen *recruitment ratio* based on the number of young aspen stems (≤ 5 cm DBH) to the number of mature aspen stems (≥ 6 cm DBH). This allows researchers and managers to quickly assess and classify stands as stable or decreasing at a single point in time. The ratio can be an effective measure of current recruitment. A recruitment ratio of ≥ 1.0 indicates aspen stands that are remaining stable or increasing in size. A recruitment ratio of < 1.0 indicates that a stand may not be able to replace itself and persist in time. To evaluate aspen persistence status in our study area, we calculated a recruitment ratio for each stand.

All sprout and DBH measurements were taken between 1 August and 15 October, 2008. To sample aspen sprouts, we evenly positioned 2 m-wide belt transects perpendicular to the short axis of each stand, beginning at the edge of the aspen stand, and continuing directionally through the stand to the other edge. We placed 1 transect in stands with an axis ≤ 50 m in length; 2 transects in stands with an axis length between 51-100 m; and 3 transects in stands with an axis length > 100 m. In each transect, we measured aspen sprout height for 2007 and 2008, overstory shading (densitometer), conifer basal area, and aspen basal area. All aspen sprouts within transects were classified as *browsed* (apical growth eaten by a large herbivore), *diseased* (apical growth terminated by disease), or *intact* (unbrowsed/non-diseased) for year 2007 and 2008. Aspen shoot blight (ASB) caused by *Pollaccia americana* Ondrej, also known as shepherds crook, is the most common disease found in quaking aspen (Hinds, 1985; Blenis, 2007). We identified the presence of ASB in our study area, occurring in every aspen stand.

Fences and Jackstraw

For our study, we defined *jackstraw* as more than one log lying on another in a fashion that creates a physical barrier of any height on two or three sides of a triangle around an aspen sprout or stem. All coarse woody debris that met the definition was considered to be jackstraw, regardless of height. All recently recruited aspen stems ($\leq$ 5 cm DBH) were categorized as behind jackstraw or accessible to herbivores.

We used a split-plot design to test herbivory and disease effects on sprout heights inside and outside herbivore barriers (jackstraw or fencing). Our whole plots were jackstraw and fencing. We randomly selected 4 of the 8 stands that contained jackstraw. If a stand was chosen that occurred within 400 m of an already selected stand, it was considered spatially correlated and another stand was selected. We included both stands on the neighboring district that contained fencing. Since the refugium campground stand contained fencing, we measured it as a control to test our null hypothesis that there would be no sprout height difference inside and outside the barrier. For each of the fenced stands, we randomly selected a section of fencing. Similarly, within each of the four jackstraw stands, we randomly selected a jackstraw pile. Belt transects were placed inside and outside the jackstraw and fencing. We used 2 m x 10 m transects for jackstraw. For fences, we used 2 m wide transects that ran the length of the fence. In each transect, we measured aspen sprout height for 2007 and 2008, overstory shading (densitometer), conifer basal area, and aspen basal area. As in our stand-level transects, we characterized each aspen sprout as browsed, diseased, or intact for 2007 and 2008.

Data Analysis

We used S-PLUS 8.0 statistical software (Insightful Corp, Seattle, Washington) for all our analyses. For our age-diameter relationship, we used a simple linear regression model (SLR). We tested the effects of conifer basal area on sprout densities using a SLR after we added 0.05 to sprouts/m^2 and performed a natural log transformation. Herbivory effects on sprout height was analyzed statistically using a liner mixed effect model (LME), with sprout height (cm) as the response variable, and barrier type (jackstraw or fence), and sprout location (inside/outside) and their interaction as explanatory variables. Barrier ID (1-8) and sprout location in barrier ID were included as random effects to account for observations not being independent from one another. LME models distinguish within-plot sources of variation from between-plot sources of variation. Observations sharing the same random effect are autocorrelated (Pinherio and Bates, 2000). We tested this model for all sprouts for year 2007, and separately for diseased sprouts for year 2007. One of the 4 jackstraw barriers was removed from the disease comparison because it lacked diseased sprouts on one side of the barrier. For comparison, we tested sprout heights inside and outside of the fence in the refugium stand with a pooled-variance two-sample *t*-test under the prediction that there would be no difference.

RESULTS

We measured a total of 16 aspen stands. Mean aspen stand size for the 13 herbivore accessible stands was 0.3 ha (range: 0.1 to 0.6 ha). The refugium was 0.4 ha and the two fenced stands were 0.2 ha and 0.6 ha in size. In our complete enumeration of all trees ≥ 2.5 m within our selected stands, we collected a total of 439 aspen stem DBH measurements and 4,120 conifer trees DBH measurements. The linear relationship between age (years) and diameter (cm) for aspen stems in our study area was $y = 2.32x + 4.2$ (SLR: $r^2 = 0.85$, p-value < 0.001, *standard error* (*SE*) = 5.9, n = 67; Figure 2.7). Six years were added to each age based on the average years it took 18 sprouts we sampled from four stands to reach breast height (Mean = 6 yrs, *standard deviation (SD)* = 2). Our final age-diameter relationship was: Establishment Year = 2008 – (2.32 * DBH) + 4.2 + 6. Ponderosa pine and lodgepole pine establishment years were calculated using equations from a study near our refugium and fenced stands (Chalyon Shuffield, unpublished data).

Histograms of aspen stem frequency and establishment decade show that missing age classes began in the 1960s and continued through the 1990s when compared to local refugium and expected recruitment (Figure 2.2). Stems protected by jackstraw provided an exception to this. More than 75% of all stems that had recently recruited into the overstory (≤ 5 cm DBH; < 20 years) in our study area occurred behind jackstraw (Figure 2.2). Ponderosa pine in our aspen stand areas established as early as the late 1600s, increasing in the 1930s through 1970s (Figure 2.3). Similarly, lodgepole pine established in the late 1800s, increasing in the 1920s before a significant increase in the 1960s and 1970s (Figure 2.3).

Only stands with jackstraw had a recruitment ratio ≥ 1.0. Six (46%) of the 13 aspen stands had a recruitment ratio ≥ 1.0 (range: 1.3 to 14.5). Eight (62%) of the stands had a ratio of < 1.0 and therefore were considered unstable or declining. The refugium had a ratio of 2.5. The two stands with fences had recruitment ratios of 9.5 and 12.9. In general, stands with jackstraw had higher stem recruitment, less herbivory, and taller sprouts than stands without jackstraw.

We found 376 aspen sprouts within the 26 transects situated in the 13 aspen stands in our study area (Table 2.0). The mean sprout density was 5,894 per ha (range: 1,087 – 22,900 sprouts/ha). The mean sprout height was 56 cm (range: 39–103 cm). An average of 37% (*SE* ± 6) of sprouts were browsed (range: 9–75%) and 38% (*SE* ± 5) were diseased (range: 15– 81%). When these two categories were combined, the percentage of sprouts browsed or diseased was high at the landscape (75%, *SE* ± 4) and the stand level (range: 50–100%; Table 2.0). Jackstraw in our study area had a mean height of 0.54 m (*SD* = 0.13 m). All fences were all 2.5 m in height.

In our split-plot design, we measured 288 aspen sprouts and found heights were significantly different between sprouts accessible to herbivores and sprouts protected by a barrier (LME: $F_{1,4} = 52.8$, *p*-value < 0.002). The magnitude of difference depended on the barrier type, with the fencing having a greater difference. The median sprout height inside the fence was 7.6 times taller than the median sprout height outside (95% CI = 5.9 and 9.7; Figure 2.6). The median sprout height inside jackstraw was 2.4 times taller than the median sprout height outside (95% CI = 1.6 and 3.4; Figure 2.6). Variation of sprout heights within sites was more than variation among sites. In contrast, sprout heights inside and outside the refugium fence did not differ (two-sample t-test: *n* = 90; *p*-value < 0.001).

In a subset of 112 diseased sprouts in our split-plot design, we found disease alone did not suppress aspen sprout height when the sprouts were protected from herbivory. There was convincing evidence that diseased aspen sprout heights inside the barriers (jackstraws and fences) differ from those outside (LME: $F_{1,4} = 112$, *p*-value < 0.0001). The median aspen sprout height inside the barrier was 5.6 times taller than the median sprout height accessible to herbivores (95% CI = 3.7 and 8.3). Variation of sprout heights within sites was more than variation among sites.

Aspen sprout density increased as conifer basal area decreased (Figure 2.4). We found moderate evidence that log of aspen sprout density was negatively correlated to conifer basal area (SLR: $F_{1,13} = 5.02$, *p*-value = 0.04). Aspen sprout density increased by 1.5 times for every conifer basal area decrease of 10 m^2/ha (95% CI = 1.0 and 2.4).

We found no significant correlation between conifer basal area and recent aspen recruitment (≤ 5 cm DBH; *p*-value = 0.19), aspen basal area and aspen sprout density (*p*-values = 0.18), nor total basal area and aspen sprout density (*p*-value = 0.29) for 2008. Total canopy cover, as measured with a densitometer, and aspen sprout density also had no correlation for 2008 (*p*-value = 0.99).

DISCUSSION

Similar to other areas in the western US, we found aspen overstory recruitment declining across the last half a century (Kay, 1997b; White *et al.*, 1998; Ripple and Larsen, 2000; Bartos, 2001; Di Orio *et al.*, 2005; Jones *et al.*, 2005; Kaye *et al.*, 2005). We found clear negative relationships between: (1) aspen overstory stem recruitment and herbivore accessibility; (2) aspen sprout height and herbivory; and (3) aspen sprout density and conifer basal area.

Soon after active fire suppression in the 1920s, conifer overstory increased significantly for the next 50-years (Figure 2.3). Fire-dependant ponderosa pine forests evolved with frequent low severity fires that maintained open, well-spaced large diameter trees (Agee, 1993). In our study area, ponderosa pine and lodgepole pine occurred in densities greater than aspen in aspen stand areas (Figure 2.2 and 2.3). The presence of conifers predates current aspen stems by 400 years in some stands even though the aspen clone may be much older. Conifer densities, however, remained low until 1930s. While co-occurrence has likely existed for centuries, the dry, fire-dependent forest had a low MFRI and little to no encroachment until active and passive fire suppression (Bork, 1985). In the Rocky Mountains, aspen stands were found in small patches in lower elevation ponderosa pine where low severity fire did not allow the aspen to form into parklands (Kaye *et al.*, 2003). Additionally, aspen stands have been noted as part of the most common ponderosa pine habitat types (Thilenius, 1972; Shepperd and Battaglia, 2002) and a component of primarily pure ponderosa pine forest (Abella, 2005). We suggest that for the last 600 hundred years within our study area, some aspen stands were persisting within mature ponderosa or mixed pine stands. Historical fires were frequent and of low severity (Bork, 1985). We observed geographic features, such as meandering drainages and mesic sites, within dry ponderosa pine stands that could slow low severity fires and therefore allow aspen stems to persist until larger fire events. In our study area, some aspen stands have been recruiting for nearly 200 years near large-diameter ponderosa pine trees (Figures 2.1 and 2.2). This recruitment decreased when heavy conifer encroachment competed with aspen and decreased forage for ungulates.

Aspen overstory recruitment decreased in herbivore accessible stands for 30-years from the 1960s to 1980s in comparison to the refugium and expected recruitment within small stands (Figure 2.2). This decline occurred after a half-century of fire suppression (Agee, 1993) and more than three decades of an irruptive mule deer population (Salwasser, 1979). Aspen overstory recruitment increased and returned to expected recruitment levels in the 1990s following more than a decade of pine-bark beetle outbreak in our study area (Williams and Liebhold, 2002) that killed the encroaching lodgepole pine and subsequently created jackstraw. Aspen overstory recruitment did not occur uniformly in our study area, as more than 75% of all recently recruited stems (< 20 years) were behind jackstraw. We therefore suggest that ungulate herbivory in conjunction with conifer encroachment was suppressing aspen stems and sprouts in our study area.

Release of overstory trees in aspen stands increases soil temperature and solar radiation (Carlson and Groot, 1997) and allows aspen stems to grow 2-3 times more dense than under full overstory (Cumming *et al.*, 2000). Over 90% of beetle-killed lodgepole pine snags fall within a decade (Mitchell and Preisler, 1998), thereby increasing coarse woody debris, which can act as an herbivore barrier to ungulates (Ripple and Larsen, 2001). While deer numbers decreased in our study area (Salwasser, 1979; Peek *et al.*, 2002), elk and livestock numbers did not. Conifer encroachment increased in our study area, decreased aspen sprout density (Figure 2.3 and 2.4) and decreased available forage (Peek *et al.*, 2001) for domestic and wild ungulates. This put more herbivory pressure on the remaining aspen sprouts.

We found aspen sprouts behind jackstraw recruited into the overstory (Figure 2.2) and were 2.4 times taller than sprouts not protected from ungulates (Figure 2.6). Our findings are similar to other studies of coarse woody debris protecting sprouts from herbivores (Reynolds, 1969; Ripple and Larsen, 2001; Kota, 2005; Chantal and Granström, 2007) and are similar to fenced stands in our study (Figure 2.6) and other studies (Baker *et al.*, 1997; Kay, 2001). However, as reported elsewhere (Forester *et al.*, 2007), jackstraw did not have a uniform effect when examined across the landscape. Two (25%) of the 8 stands in our study area that contained jackstraw had recruitment ratios of < 1.0, leaving only 46% of stands in our study area as stable or increasing. Nonetheless, the stem recruitment that did occur behind jackstraw was at a high enough level for aspen to persist at the landscape scale (Figure 2.2).

Small aspen stands tend to recruit overstory across time through small openings (Cumming *et al.*, 2000), thus allowing stands to persist between disturbance events (Kay, 1997a). We propose that mountain pine beetle outbreaks such as occurred in Central Oregon in the 1980s and 1990s can act as that disturbance event, and as such: (1) remove conifer shading and resource competition; (2) create snags, and subsequent increase in CWD piles which acts as an herbivore barrier; and (3) therefore increase sprout density and heights, which leads to overstory recruitment. Thus, we suggest that the mountain pine beetle has provided an ecosystem service and further, has a powerful ecological effect that can help aspen recruit at the stand level and persist at the landscape level.

CONCLUSION

Our results indicate that in order to persist, aspen stands on the eastern slope of the Central Oregon Cascades need disturbance that decreases overstory competition from conifers and ungulate accessibility to aspen sprouts. Aspen sprouts and recently recruited aspen stems occurred at expected levels even in the absence of fire, suggesting that mature aspen stems can remain intact and the stand can still expand and persist (Kay, 2001). The small aspen stands ($\leq$ 0.6 ha) we found were spatially correlated in clusters (2-3 stands $\leq$ 30 m apart) embedded in a dense conifer matrix. Each cluster could have been a single, larger stand when conifer basal area and ungulate browsing pressure were less (Di Orio *et al.*, 2005). Conifer removal would increase aspen sprout density and decrease competition with mature aspen stems. However, some of the aspen stands have recruited across time under large-diameter ponderosa and lodgepole pine, showing that fire-tolerant ponderosa pine may co-exist with aspen in some environments. Although ungulates do not overwinter in our study area, aspen overstory still decreased across time. Much emphasis has been put on winter browse and damage to aspen by elk (Baker *et al.*, 1997; White *et al.*, 1998; Ripple and Larsen, 2000). Our study shows that summer and fall browse of aspen sprouts, in conjunction with and apart from conifer encroachment, can still suppress aspen overstory recruitment. Unless herbivory pressure is altered (e.g., grazing rotation, barriers), we caution against cutting the aspen overstory to increase sprout density. The lack of ungulates in the winter may have allowed lower jackstraw height (mean = 0.54 m) to be as effective as fencing (2.5 m). This could aid managers in herbivory exclusion approaches.

The beetle-killed lodgepole pine provided a disturbance similar to conifer removal and fencing, suggesting that managers could use or create “natural fencing” made of downed conifers to allow aspen recruitment and persistence. In our study area, the occurrence of jackstraw in each stand was more random than fencing and excluded herbivory in part of, but not the entire stand. This partial exclusion may serve a key role in aspen ecosystem restoration by allowing continued wildlife access to the stand, decreasing stem exclusion, and increasing stand heterogeneity.

Managers should consider jackstraw as one option in aspen restoration. Further research into jackstraw density and recruitment ratio would help scientists and managers better understand this interaction at the stand level. In addition, future research should consider other vegetative responses behind jackstraw, such as herbs and forbs, in comparison to fenced stands. The creation of a jackstraw metric (height and density) would allow more detailed prescription for aspen ecosystem restoration. It would be important to note that an increase in CWD could also increase an aspen stands probability of burning at higher severity. Additionally, future research should consider increasing our understanding of aspen persisting under mature pine in areas with a low MFRI.

This is an observational study and its scope of inference is limited to aspen stands in the eastern Oregon Cascades; however our findings about the effects of herbivory deterrents on aspen persistence build on studies conducted in other areas, and therefore may have relevance to scientists and managers on a wider geographic scale.

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LITERATURE CITED

Abella, S.R., 2005. Environmental and vegetational gradients on an Arizona ponderosa pine landscape: implications for ecological restoration. Doctoral dissertation, Northern Arizona University, Flagstaff, AZ. 184 pp.

Agee, J.K., 1993. Fire Ecology of Pacific Northwest Forests, Island Press, Washington, DC (1993) 493 pp.

Applequist, M.B., 1958. A simple pith locator for use with off-center increment cores. J For 56, 141.

Bailey, J.K., Whitham, T.G., 2002. Interactions among Fire, Aspen, and Elk Affect Insect Diversity: Reversal of a Community Response. Ecology 83, 1701-1712.

Bailey, V., 1936. *The mammals and life zones of Oregon.* N Am Fauna 55, 416 pp.

Baker, W.L., Munroe, J.A., Hessl, A.E., 1997. The effects of elk on aspen in the winter range in Rocky Mountain National Park. Ecography 20, 155-165.

Bartos, D.L., 2001. Landscape dynamics of aspen and conifer forests.

Bates, J.D., Miller, R.F., Davies, K.W., 2006. Restoration of Quaking Aspen Woodlands Invaded by Western Juniper. Rangeland Ecology and Management 59, 88-97.

Betters, D.R., Woods, R.F., 1981. Uneven-Aged Stand Structure and Growth of Rocky Mountain Aspen. J For 79, 673-676.

Blenis, P.V., 2007. Impact of simulated aspen shoot blight on trembling aspen. Can J For Res 37, 719-725.

Bork, J., 1985. Fire history in three vegetation types on the east side of the Oregon Cascades. Ph.D. Dissertation. Oregon State University, Corvallis, OR.

Brown, K., Hansen, A., Keane, R., Graumlich, L., 2006. Complex interactions shaping aspen dynamics in the Greater Yellowstone Ecosystem. Landsc Ecol 21, 933-951.

Carlson, D.W., Groot, A., 1997. Microclimate of clear-cut, forest interior, and small openings in trembling aspen forest. Agricultural and Forest Meteorology 87, 313-329.

Chantal, M.d., Granström, A., 2007. Aggregations of dead wood after wildfire act as browsing refugia for seedlings of Populus tremula and Salix caprea. For Ecol Manage 250, 3-8.

Chong, G.W., Simonson, S.E., Stohlgren, T.J., Kalkhan, M.A., 2001. Biodiversity: aspen stands have the lead, but will nonnative species take over? Pages 261–271 in W. D. Shepperd, D. Binkley, D. L. Bartos, T. J. Thomas, and L. G. Eskew, compilers. Sustaining aspen in western landscapes: Symposium Proceedings. USDA Forest Service Rocky Mountain Research Station, RMRS-P-18, Grand Junction, Colorado.

Cumming, S.G., Schmiegelow, F.K.A., Burton, P.J., 2000. Gap Dynamics in Boreal Aspen Stands: Is the Forest Older Than We Think? Ecol Appl 10, 744-759.

Debyle, N.V., 1985a. Animal Impacts *in* Aspen: Ecology and management in the western United States. General Technical Report RM-119., Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, 115-123.

Debyle, N.V., 1985b. Wildlife *in* Aspen: Ecology and management in the western United States. General Technical Report RM-119., Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, 135-152.

Debyle, N.V., Winokur, R.P., 1985. Aspen: Ecology and management in the western United States. General Technical Report RM-119., Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, 283p.

Di Orio, A.P., Callas, R., Schaefer, R.J., 2005. Forty-eight year decline and fragmentation of aspen (Populus tremuloides) in the South Warner Mountains of California. For Ecol Manage 206, 307-313.

Flack, D.J.A., 1976. Bird populations of aspen forests in western North America. Ornithol Monogr 19, 1-97.

Forester, J.D., Anderson, D.P., Turner, M.G., 2007. Do high-density patches of coarse wood and regenerating saplings create browsing refugia for aspen (Populus tremuloides Michx.) in Yellowstone National Park (USA)? For Ecol Manage 253, 211-219.

Gitlin, A.R., Sthultz, C.M., Bowker, M.A., Stumpf, S., Paxton, K.L., Kennedy, K., Muñoz, A., Bailey, J.K., Whitham, T.G., 2006. Mortality Gradients within and among Dominant Plant Populations as Barometers of Ecosystem Change During Extreme Drought. Conserv Biol 20, 1477-1486.

Harper, J.A., 1985. Ecology and management of Roosevelt elk in Oregon. Oregon Department of Fish and Wildlife, Portland, Oregon., 70 pp.

Hessburg, P.F., Agee, J.K., 2003. An environmental narrative of Inland Northwest United States forests, 1800-2000. For Ecol Manage 178, 23-59.

Hinds, T.E., 1985. Diseases. Pages 87–114 in N. V. DeByle and R. P. Winokur, editors. Aspen: ecology and management in the western United States. USDA General Technical Report RM-119.

Hogg, E.H.T.e.d., Brandt, J.P., Michaelian, M., 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Can J For Res 38, 1373-1384.

Johnson, N.K., Franklin, J.F., 2009. Restoration of Federal Forests in the Pacific Northwest: Strategies and Management Implications. Special report to Senator Wyden and Congressman DeFazio., 120 pp.

Jones, B.E., Rickman, T.H., Vazquez, A., Sado, Y., Tate, K.W., 2005. Removal of encroaching conifers to regenerate degraded aspen stands in the Sierra Nevada. Restor Ecol 13, 373-379.

Kashian, D.M., Romme, W.H., Regan, C.M., 2007. Reconciling Divergent Interpretations of Quaking Aspen Decline on the Northern Colorado Front Range. Ecol Appl 17, 1296-1311.

Kay, C.E., 1985. Aspen Reproduction in the Yellowstone Park - Jackson Hole Area and its Relationship to the Natural Regulation of Ungulates. in Workman, G.W. (ed.), Western Elk Management: A Symposium, Utah State University, Logan.

Kay, C.E., 1997a. The condition and trend of aspen in Kootenay and Yoho National Parks: implications for ecological integrity. Canadian Field Naturalist 111, 607–616.

Kay, C.E., 1997b. Is Aspen Doomed? J For 95, 4-11.

Kay, C.E., 2001. Long-term aspen exclosures in Yellowstone ecosystem. Pages 225–240 in W. D. Shepperd, D. Binkley, D. L. Bartos, and T. J. Stohlgren, compilers. Sustaining aspen in western landscapes: symposium proceedings, 13– 15 June 2000, Grand Junction, Colorado. USDA Forest Service, RMRS-P-18. Fort Collins, Colorado, USA.

Kaye, M., Stohlgren, T., Binkley, D., 2003. Aspen structure and variability in Rocky Mountain National Park, Colorado, USA. Landsc Ecol 18, 591-603.

Kaye, M.W., Binkley, D., Stohlgren, T.J., 2005. Effects of Conifers and Elk Browsing on Quaking Aspen Forests in the Central Rocky Mountains, USA. Ecol Appl 15, 1284-1295.

Keyser, T.L., Smith, F.W., Shepperd, W.D., 2005. Trembling aspen response to a mixed-severity wildfire in the Black Hills, South Dakota, USA. Can J For Res 35, 2679-2684.

Kota, A.M., 2005. Fences and on-site forest materials as ungulate barriers to promote aspen persistence in the Black Hills. M.S. thesis, Utah State University, Logan, UT, 74 pages.

Kulakowski, D., Veblen, T.T., Drinkwater, S., 2004. The Persistence of Quaking Aspen (Populus Tremuloides) in the Grand Mesa Area, Colorado. Ecol Appl 14, 1603-1614.

Larsson, S., Oren, R., Waring, R.H., Barrett, J.W., 1983. Attacks of Mountain Pine Beetle as Related to Tree Vigor of Ponderosa Pine. For Sci 29, 395-402.

Little, E.L., Jr., 1971. Conifers and important hardwoods. Volume I. Atlas of United States trees. Forest Service Miscellaneous Publication Number 1146, Washington D.C., USA.

Milchunas, D.G., Noy-Meir, I., 2002. Grazing refuges, external avoidance of herbivory and plant diversity. Oikos 99, 113-130.

Miller, R.E., Rose, J.A., 1995. Historic Expansion of Juniperus-Occidentalis (Western Juniper) in Southeastern Oregon. Great Basin Nat 55, 37-45.

Mitchell, R.G., Preisler, H.K., 1998. Fall Rate of Lodgepole Pine Killed by the Mountain Pine Beetle in Central Oregon. West J Appl For 13, 23-26.

Mueggler, W.F., 1985. Vegetation associations. Pages 45–55 in N. V. DeByle and R. P. Winokur, editors. Aspen: ecology and management in the western United States. General Technical Report RM-119. United States Department of Agriculture Forest Service, Fort Collins, Colorado, USA.

Oaten, D.K., Larsen, K.W., 2009. Aspen Stands as Small Mammal "Hotspots" Within Dry Forest Ecosystems of British Columbia. Northwest Sci 82, 276-285.

ODFW, 2003a. Oregon's Elk Management Plan. Oregon Department of Fish and Wildlife, Portland, Oregon., 63 pp.

ODFW, 2003b. Oregon's Mule Deer Management Plan. Oregon Department of Fish and Wildlife, Portland, Oregon., 29 pp.

ODFW, 2006. Aspen Woodlands, in Oregon Conservation Strategy. Oregon Department of Fish and Wildlife, Salem, Oregon. , 259-260.

Peek, J.M., Dennis, B., Hershey, T., 2002. Predicting Population Trends of Mule Deer. The Journal of Wildlife Management 66, 729-736.

Peek, J.M., Korol, J.J., Gay, D., Hershey, T., 2001. Overstory-understory biomass changes over a 35-year period in southcentral Oregon. For Ecol Manage 150, 267-277.

Pinherio, J.C., Bates, D.M., 2000. Mixed-effect Models in S and S-PLUS. New York: Springer.

Rehfeldt, G.E., Ferguson, D.E., Crookston, N.L., 2009. Aspen, climate, and sudden decline in western USA. For Ecol Manage 258, 2353-2364.

Reynolds, H.G., 1969. Aspen grove use by deer, elk, and cattle in southwestern coniferous forests. United States Department of Agriculture Forest Service, Research Paper RM-138.

Ripple, W.J., Beschta, R.L., 2005. Refugia from browsing as reference sites for restoration planning. West N Am Nat 65, 269-273.

Ripple, W.J., Beschta, R.L., 2007. Restoring Yellowstone's aspen with wolves. Biol Conserv 138, 514-519.

Ripple, W.J., Larsen, E.J., 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. Biol Conserv 95, 361-370.

Ripple, W.J., Larsen, E.J., 2001. The Role of Postfire Coarse Woody Debris in Aspen Regeneration. West J Appl For 16, 61-64.

Romme, W.H., Turner, M.G., Tuskan, G.A., Reed, R.A., 2005. Establishment, Persistence, and Growth of Aspen (Populus tremuloides) Seedlings in Yellowstone National Park. Ecology 86, 404-418.

Romme, W.H., Turner, M.G., Wallace, L.L., Walker, J.S., 1995. Aspen, Elk, and Fire in Northern Yellowstone Park. Ecology 76, 2097-2106.

Rumble, M.A., Pella, T., Sharps, J.C., Carter, A.V., Parrish, B.J., 1996. Effects of logging slash on aspen regeneration in grazed clearcuts. The Prairie Naturalist 28, 199–209.

Salwasser, H., 1979. The ecology and management of the Devil’s Garden Interstate Deer Herd and its range. Ph.D. Dissertation, University of California (Berkeley).

Schier, G.A., Jones, J.R., Winokur, R.P., 1985. Vegetative regeneration. In: N. V. DeByle and R. P. Winokur, eds. Aspen: ecology and management in the western United States. USDA, For. Serv. Rocky Mountain Forest and Range Experiment Station. Fort Collins, CO. Gen. Tech. Rep RM-119: 20–33.

Shepperd, W.D., Battaglia, M.A., 2002. Ecology, siliviculture, and management of Black Hills ponderosa pine. Gen. Tech. Rep. RMRS-GTR-97. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 112 p.

Shirley, D.M., Erickson, V., 2001. Aspen restoration in the Blue Mountains of Northeast Oregon. Pages 101-115 in Shepperd et al., compilers. Sustaining aspen in western landscapes: Symposium Proceedings. USDA Forest Service Rocky Mountain Research Station, RMRSP- 18, Grand Junction, Colorado.

Stokes, M.A., Smiley, T.L., 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago.

Thilenius, J.F., 1972. Classification of deer habitat in the ponderosa pine forest of the Black Hills, South Dakota. Res. Pap. RM-91. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, 28 p.

Verts, B.J., Carraway, L.N., 1998. Land Mammals of Oregon. University of California Press, Berkeley, CA, 668.

Wall, T.G., Miller, R.F., Svejcar, T.J., 2001. Juniper encroachment into aspen in the Northwest Great Basin. J Range Manage 54, 691-698.

White, C.A., Olmsted, C.E., Kay, C.E., 1998. Aspen, Elk, and Fire in the Rocky Mountain National Parks of North America. Wildl Soc Bull 26, 449-462.

Williams, D.W., Liebhold, A.M., 2002. Climate change and the outbreak ranges of two North American bark beetles. Agric For Entomol 4, 87-99.

Worrall, J.J., Egeland, L., Eager, T., Mask, R.A., Johnson, E.W., Kemp, P.A., Shepperd, W.D., 2008. Rapid mortality of Populus tremuloides in southwestern Colorado, USA. For Ecol Manage 255, 686-696.

Zalunardo, R.A., 1965. The Seasonal Distribution of a Migratory Mule Deer Herd. The Journal of Wildlife Management 29, 345-351.

Figure 2.1. Map of east Cascades study area. Fremont-Winema National Forest highlighted.

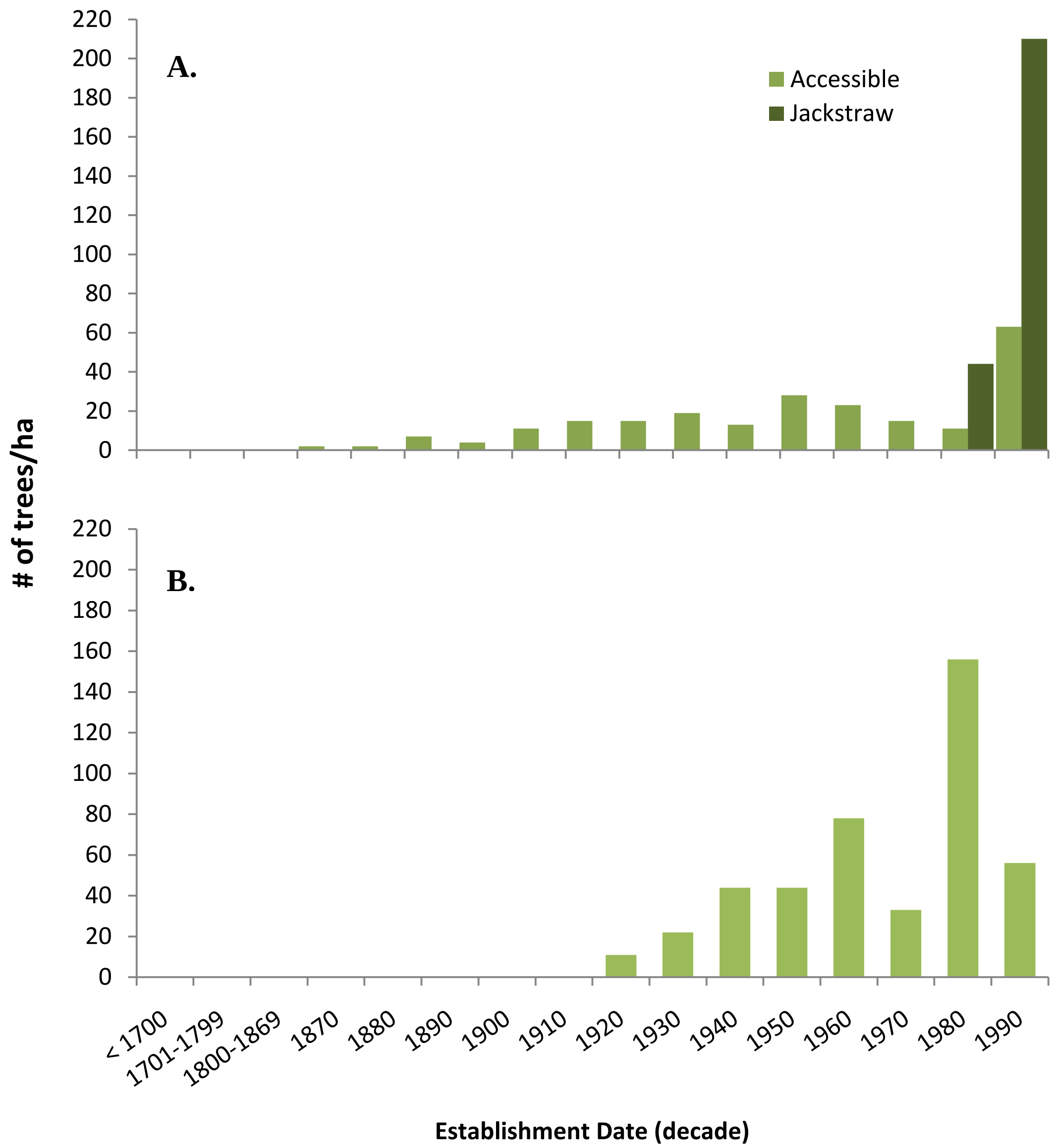

Figure 2.2. Aspen age structure from before 1700 to 1999 for trees ≥ 2.5 m high. (A) Herbivore-accessible stands (*n* =13) some stands (*n* = 8) had jackstraw excluding herbivores from part of the area. Aspen recruiting behind jackstraw are noted in darker green. (B) Refugium stand (*n* = 1) showing expected recruitment over time, with alternating decadal pulse seen in single stands.

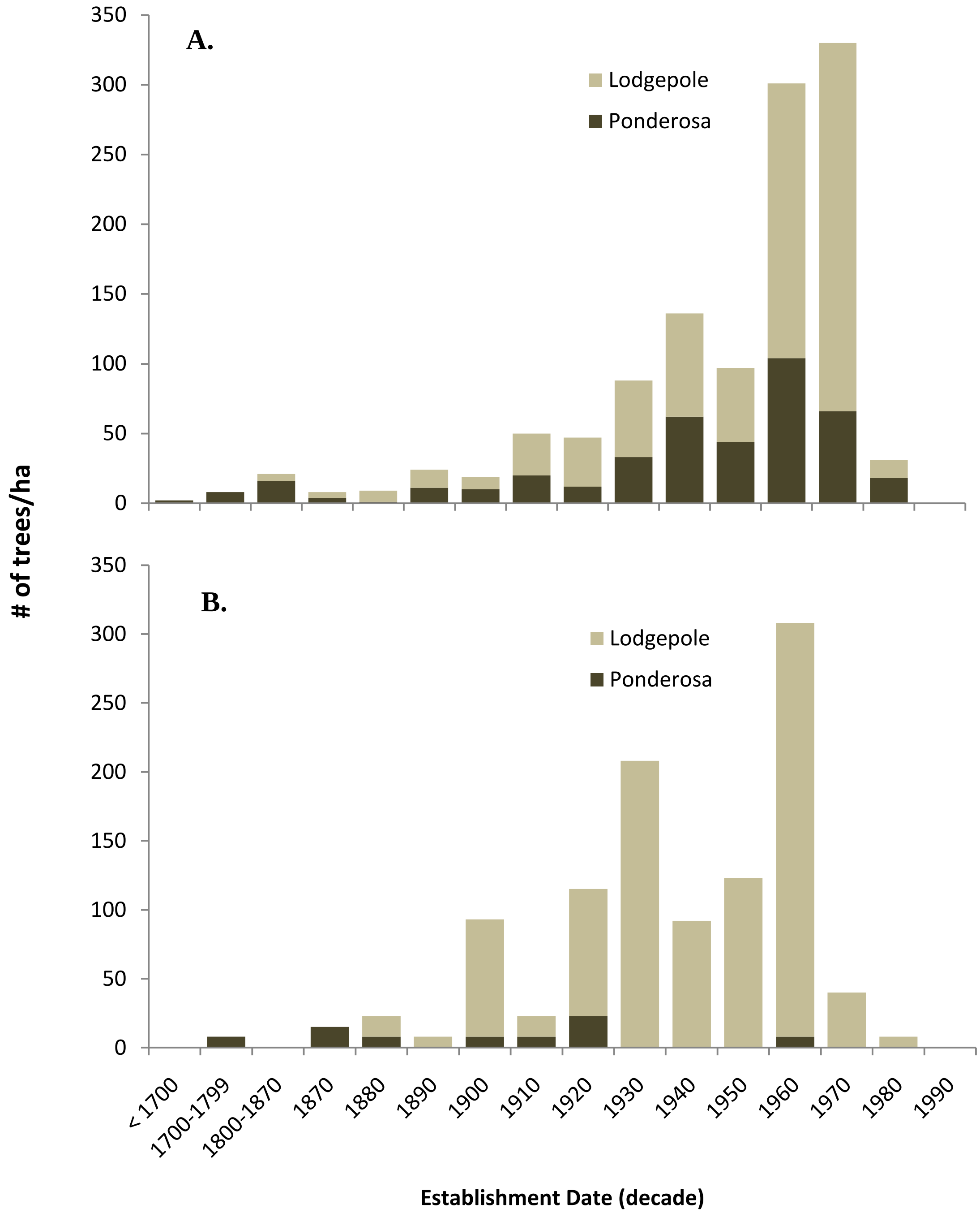

Figure 2.3. Coniferous trees age-structure for average number of ponderosa and lodgepole pine trees growing within aspen stand areas. (A) Herbivore accessible stands (*n* = 13), and (B) Refugium stand (*n* = 1).

Table 2.1 Aspen characteristics in the herbivore accessible and refugium stands

Variable	**Accessible Stands (*n*=13)**	**Refugium (*n*=1)**
Sprout height (cm) 2007 mean (*standard deviation*)	56 (±16)	77
Annual growth of intact sprouts[1] (cm) 2008 mean (*standard deviation*)	16 (±2)	20
% Sprouts >1m 2007	16%	32%
% Browsed (ungulate) 2007	40%	1%
% Diseased 2007	45%	37%

[1] sprouts that were not browsed or diseased

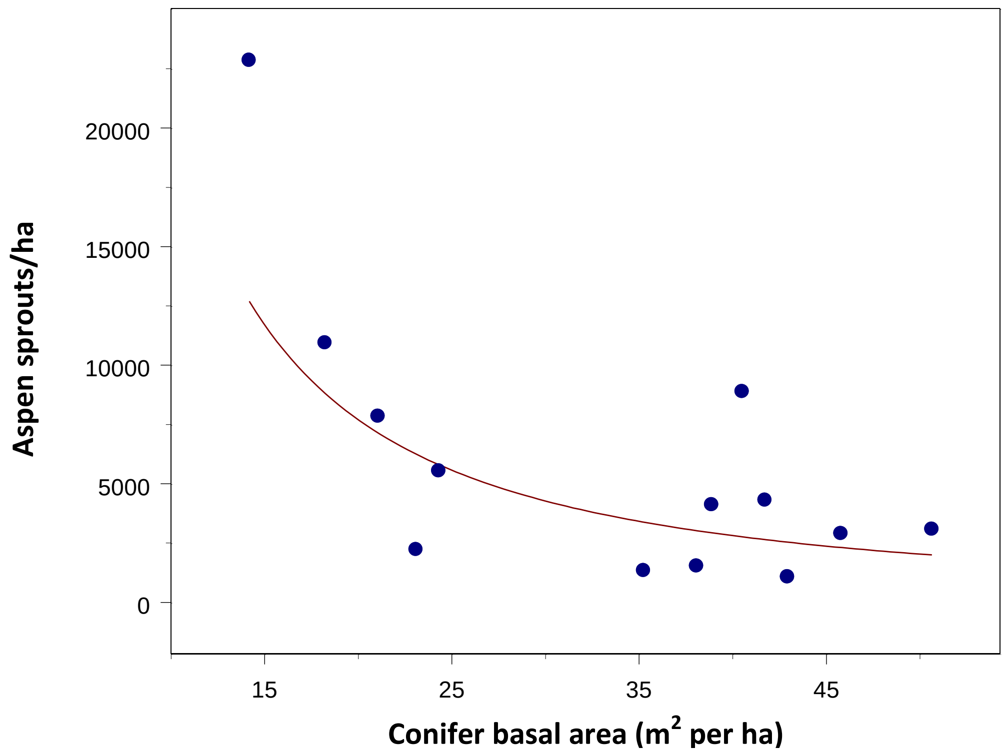

Figure 2.4. Aspen sprout density (per ha) in relation to conifer basal area (m^2/ha) for aspen stand areas (*n* = 13).

Figure 2.5. Aspen exclosure on the Deschutes National Forest showing dense recruitment of aspen trees inside the 10-year old exclosure and suppressed sprouts outside. The fence is approximately 2.5 meters tall.

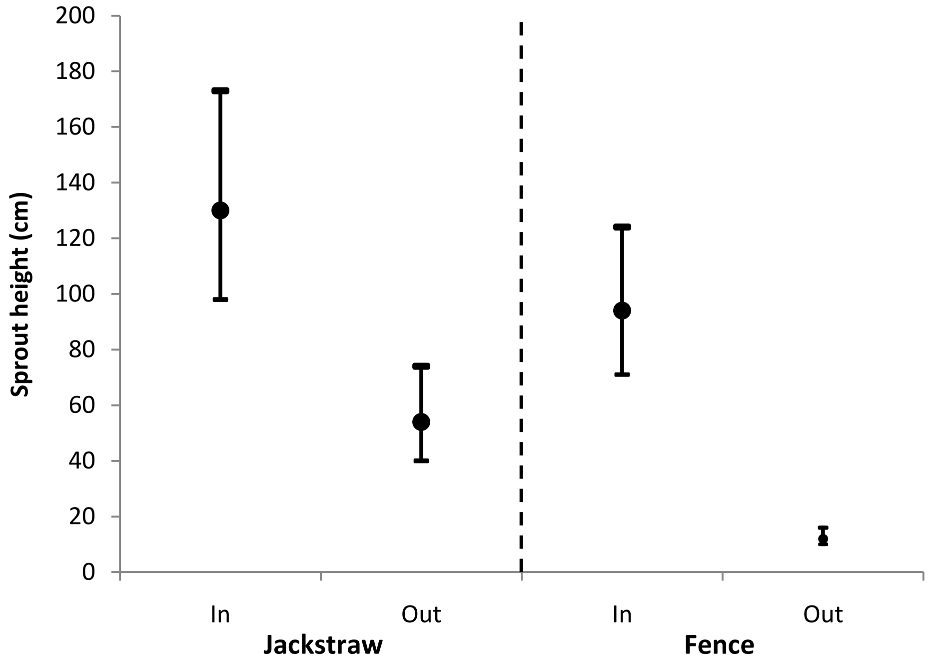

Figure 2.6. Median sprout heights inside and outside of herbivore barriers (jackstraw and fence). For jackstraw, median sprout height: inside was 130 cm (95% CI = 98 and 173) and outside was 54 cm (95% CI = 40 and 74). For fence, median sprout height: inside was 94 cm (95% CI = 71 and 124) and outside was 12 cm (95% CI = 10 and 16).

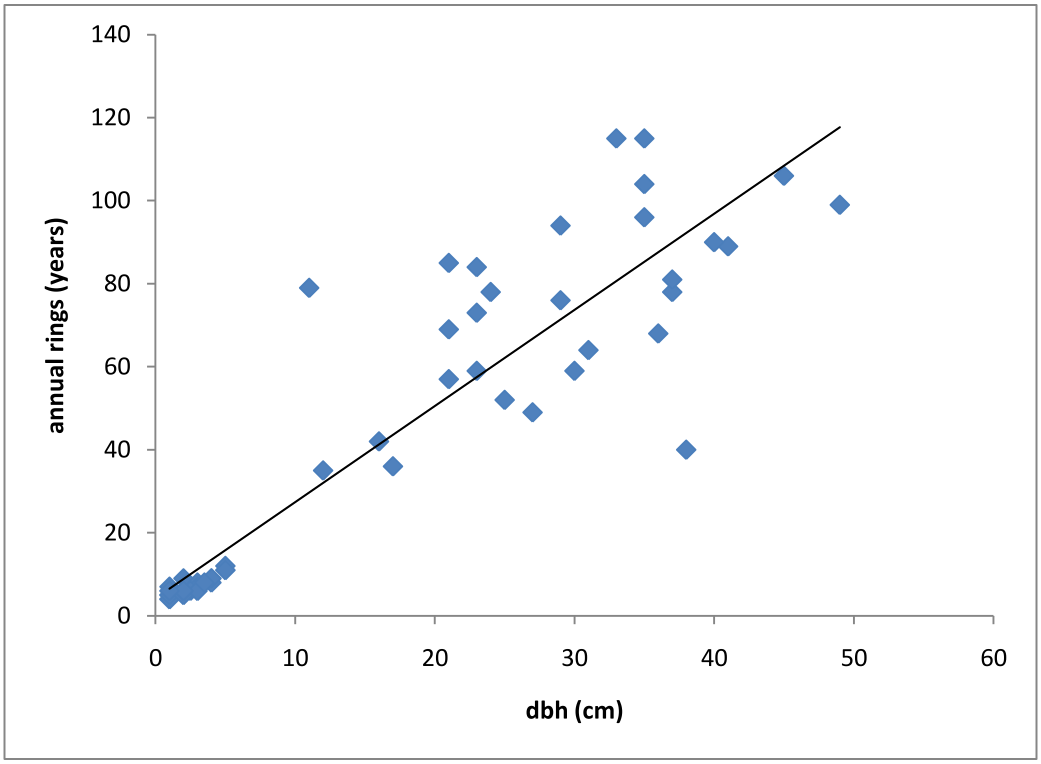

Figure 2.7. Age-diameter relationship for aspen in eastern Oregon Cascade Mountains. $y = 2.1367x + 4.1959$ ($r^2 = 0.85$, p-value < 0.001, $SE = 5.9$, $n = 67$)

CHAPTER 3 – QUAKING ASPEN (POPULUS TREMULOIDES) IN WESTERN OREGON

ABSTRACT

Quaking aspen (*Populus tremuloides* Michx.) is considered an intermountain tree species of the open range and dry forests in the western US. We report on the species outside of its expected range, in the wet temperate coniferous forests of the western slope of the Cascade Mountains and on the Willamette Valley floor, Oregon. The two landscapes receive high amounts of annual precipitation (220 and 115 cm) in comparison to that found in the range of aspen elsewhere in the state and intermountain west. We report on 16 aspen stands found on the western slope of the Cascades Mountains and in the Willamette Valley in Oregon. We censused all existing stands in these areas and classified them into 6 types: Snowfield, Upland Aspen/Conifer, Meadow Fringe, Lithic/Boulder, Pasture Valley, Riparian Valley. In this paper, we (1) describe the current status of the stand types; (2) report on our assessment of their overstory and understory; and (3) describe stressors found in each stand type. All aspen stems (overstory) and sprouts (understory) were enumerated in both landscapes.

INTRODUCTION

The most widely distributed deciduous tree in North America (Little, 1971), quaking aspen stands (*Populus tremuloides* Michx.) are considered highly important wildlife habitat in part because of associated vegetation types, soil moisture, and biodiversity in an otherwise dry intermountain west (Mueggler, 1985; White *et al.*, 1998). This biodiversity is documented across multiple food web levels and taxa including: bryophytes, lichens, and fungi (Crites and Dale, 1998), arthropods (Bailey and Whitham, 2002), avifauna (Flack, 1976; Dobkin, 1995; Griffis-Kyle and Beier, 2003), small mammals (Oaten and Larsen, 2009), and large mammals (see Debyle, 1985b; Fisher and Wilkinson, 2005 for a reviews). Unlike in most western landscapes, Shepperd and colleagues (2006) found aspen less common in the Sierra Nevada range, where it therefore may be more ecologically valuable. They reported on the aspen stand types and corresponding stressors found in this eco-region. As in other regions of the western US, aspen stands in the Sierra Nevada range were impacted by: herbivory, disease, conifer encroachment, pest and insect outbreak, lack of disturbance regimes, climate change, and water stress (Romme *et al.*, 1995; Ripple and Larsen, 2000; Bartos, 2001; Kulakowski *et al.*, 2004; Shepperd *et al.*, 2006; Worrall *et al.*, 2008).

A paucity of published research on aspen ecology and management in Oregon exists, limited in scope to the eastern portion of the state (Miller and Rose, 1995; Shirley and Erickson, 2001; Wall *et al.*, 2001). In western Oregon, aspen have been noted (Sudworth, 1908) and mapped (Little, 1971), but this species' current conservation status remains unknown, with no known studies or agency reports. The Oregon Department of Fish and Wildlife (ODFW) lists aspen stands as a critical wildlife habitat (ODFW, 2006).

In order to provide baseline information to land managers, we report on the current status and distribution of aspen stands on the western slope of the Central

Oregon Cascade Mountains and on the Willamette Valley floor. Our objectives were to (1) describe the current status of the stand types; (2) assess their overstory and understory; and (3) document and describe any stressors found in each stand type. Our findings are specific to aspen stands in our study area, but can provide insight into this species outside of its expected range.

Study Area

Our study area lies on the west slope of the Central Oregon Cascade Mountains and on the Willamette Valley floor (Figure 3.1). The aspen stands we surveyed in the mountains were on the Willamette National Forest (WNF) and approximately 80 km northeast and east of Eugene, Oregon. The elevation of the WNF ranges from 460 m to a high of 3200 m at the peak of the volcanoes, with average annual precipitation 220 cm, mostly falling as snow. The seasons are characterized as cold, wet winters and dry, warm summers. Growing season precipitation is limited to roughly 6% of annual precipitation. On the valley floor, aspen stands occurred approximately 15 km SE of Corvallis, Oregon. The average elevation of the valley is 90 m, with an average annual precipitation of 120 cm, mostly falling as rain between November and May. Growing season precipitation was around 7% of annual precipitation.

In the Cascades, there were two large herbivores in our study area, the Columbian black-tailed deer (*Odocoileus hemionus columbianus*) and Roosevelt elk (*Cervus canadensis roosevelti*). Domestic livestock numbers were low on the WNF by the mid 20th century, with a cease in sheep grazing in the late 1940s and in cattle grazing in the 1960s (Rakestraw and Rakestraw, 1991). Many small mammals occur in the mountain portion of our study area. On the valley floor, large herbivores included domestic cow (*Bos* spp.), horse (*Equus caballus*), donkey (*Equus asinus*), and sheep (*Ovis aries*). Similarly, many small mammals (native and introduced) occur on the valley floor.

Plant associations in the Cascade portion of our study area where aspen stands occurred include Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*); noble fir (*Abies procera*) and Douglas-fir; and other mixed conifer associations including white fir (*Abies concolor*), grand fir (*Abies grandis*), and western red cedar (*Thuja plicata*). Fire history of the Cascades is influenced by elevation and topography. High elevation sites with gentler topography were characterized by stand-replacing fires, with a natural fire rotation of 149 years for stand replacing fires. Lower elevation sites with steeper topography had low to moderate fire severity, with a natural fire rotation of 95 years. Fires have been less frequent since the 1900s, attributable in part to fire suppression and a shift in human land-use to agriculture (Morrison and Swanson, 1990). On the valley floor, the Kalapuya Indians probably burnt the prairies annually prior to European settlement (Boyd, 1986).

METHODS

In order to get baseline data for a species that had not been studied in the western part of Oregon, we surveyed all known aspen stands in the southern Willamette Valley and the western slope of the Oregon Cascade Mountains from

Roseburg to Portland. This included aspen stands identified by the WNF for the mountain range and by local botanists for the valley floor.

Field Methods

We defined an aspen *stem* as ≥ 2.5 m in height. This height is considered above the height to which deer and elk are able to browse young trees (Baker *et al.*, 1997). Aspen *sprouts* were clonal root suckers or seedlings < 2.5 cm in height. We defined an aspen *stand* as a group of aspen stems with an overstory of at least three stems > 8 cm diameter at breast height (DBH) located ≥ 20 m from other aspen stems. We defined the *stand area* as the polygon formed by all the aspen stems (overstory core) and the outermost sprouts (regeneration periphery), which we standardized to 10 m out from the overstory core (Keyser et al. 2005).

To create an age-diameter relationship, we cored a subset of 35 aspen stems ≥ 6 cm DBH. To represent the range of the DBH size classes in the study area, we cored at least one tree in each stand that fit in a needed size class and did not show signs of fungal or core rot, selecting these trees haphazardly. We cored the trees at a height of 1.4 m, then dried, mounted, and sanded the cores using standard dendrochronological procedures (Stokes and Smiley, 1968), and counted the annual rings using a Unislide "TA" tree-ring measuring system (Velmex, Bloomfield, New York, USA). If tree cores did not intersect the center pith, we estimated the number of missing rings using a clear sheet matching the curvature of the innermost ring in the sample (Applequist, 1958). If the cores were estimated to be missing > 10 center rings, they were not included in our analysis. Additionally, we sectioned a subset of 17 saplings ≤ 5 cm

DBH at breast height. This enabled us to age trees too small to core. We quantified an aspen age-diameter relationship from the 35 complete cores and 17 saplings. Additional years were added for the average amount of time it took 17 sprouts to reach breast height.

All aspen stems and coniferous trees ≥ 2.5 m in height within the stand were measured with a Biltmore stick. As a metric to characterize aspen stand conservation status (ability to persist over time) Kay (1985) developed an aspen *recruitment ratio* based on the number of young aspen stems (≤ 5 cm DBH) to the number of mature aspen stems (≥ 6 cm DBH). This allows researchers and managers to quickly assess and classify stands as stable or decreasing at a single point in time. The ratio can be an effective measure of current recruitment. A recruitment ratio of ≥ 1.0 indicates aspen stands that are remaining stable or increasing in size. A recruitment ratio of < 1.0 indicates that a stand may not be able to replace itself and persist in time. To evaluate aspen conservation status in our study area, we calculated a recruitment ratio for each of our stand types.

We enumerated and measured all sprouts in each stand between 1 August and 15 October 2008. Sprout height was measured for the previous and current year, and classified as *browsed* (apical growth eaten by a small or large herbivore), *diseased* (apical growth terminated by disease), or *intact* (unbrowsed/non-diseased) for each year. Additionally we noted the type of cover in which each sprout was found. For each stand, we visually estimated the percentage of cover type available. Cover types were generalized to shrub, grass, herb/forb, open understory under deciduous trees, open understory under conifer trees, and field edge. In each stand we noted any signs of small and large herbivore species.

RESULTS

We identified 16 aspen stands in our study area in western Oregon, with 6 occurring in the valley and 10 in the mountains. Of the mountain stands, one was removed from our analysis because of historical and current beaver activity, which had removed nearly all of the overstory, thereby confounding our measurements. We classified the 15 stands into 6 aspen stand types: Snowfield, Upland Aspen/Conifer, Meadow Fringe, Lithic/Boulder, Pasture Valley, and Riparian Valley (see Figure 3.2 for overstory and Figure 3.3 for photos). This classification scheme is based on previous work conducted in the Sierra Nevada range (Shepperd *et al.*, 2006).

Aspen stands in our study area were small with a mean of 0.13 ha (range: 0.004 – 0.6 ha). In our complete enumeration of aspen stems, we measured a total of 935 stems in our study area. We report on them here by stand type (Figure 3.2). The linear relationship between age (years) and diameter (cm) for aspen stems in our study area was $y = 2.21x + 0.64$ ($r^2 = 0.86$, p-value < 0.001, $SE = 9$, $n=46$). Five years were added to each age based on the average number of years it took 17 sprouts we sampled from four stands to reach breast height (Mean = 5 yrs, $SD = 1$). Our final age-diameter relationship was: Establishment Year = 2008 – (2.21 x DBH) + 0.64 + 5 (Figure 3.4).

The histograms of tree frequency and establishment decade show current aspen stems established after 1930 in all aspen types but Meadow Fringe (Figure 3.2). We estimated that establishment of stems in the Meadow Fringe began prior to 1860 in high elevation stands and in 1910 in low elevation stands. Number of stems, recruitment ratio, and number of sprouts varied with each aspen stand type (Table 3.1). Riparian Valley was the only stand type with a recruitment ratio of ≥ 1.0. All other stands are considered to be declining or unstable.

We enumerated all aspen sprouts and found 1298. Data we reported for aspen sprouts in each of the 6 aspen stand types included: height, growth, browse, and disease (Table 3.2). Aspen shoot blight (ASB) caused by *Pollaccia americana* Ondrej, also known as shepherds crook, is the most common disease found in quaking aspen (Hinds, 1985; Blenis, 2007). We identified the presence of ASB in our study area, occurring in every aspen stand type (Table 3.2). Wild ungulate (deer and elk) or small mammal browse was noted in all stand types but one, Riparian Valley (Table 3.2). Domestic livestock had access to 1 Riparian Valley stand and all 3 Pasture Valley stands. Table 3.3 contains a complete list of large and small herbivores found in the corresponding aspen stand types.

Snowfield

Snowfield aspen stands (*n*=2) had a mean size of 0.14 ha (range: 0.13 – 0.15 ha) and occurred at a high elevation (>1500 m), on steep slopes where snow caused aspen stems and sprouts to grow along the ground (see Figure 3.2-A). Stems in this stand type grew for 2-3 m horizontally along the ground before growing upward, with the corresponding lack of stem height resulting in little overstory. The understory consisted of a mix of small trees: Oregon vine maple (*Acer circinatum*), cascara (*Rhamnus purshiana*); and a shrub layer: snowberry (*Symphoricarpos albus*) with open grass/herbs/forbs that grew dense and tall over the summer. We measured 76 aspen stems, 3 aspen snags, and 2 conifers (silver fir). The recruitment ratio (0.39) signaled decreasing or unstable stands. Of the 193 sprouts, 30% were browsed, 2% were diseased, and 30% were ≥ 1 m in height for 2007. Elk sign was observed in the stands, and the sites were accessible to deer. A mountain beaver (*Aplodontia rufa)* colony inhabited one of the stands. We found evidence of large ungulates and mountain beaver herbivory on aspen sprouts (Table 3.2).

Upland Aspen/Conifer

We found only one Upland Aspen/Conifer stand in our study area. This small stand (0.005 ha) occurred on flat terrain near a road at an elevation of 1132 m. In this stand, the conifers had overtopped most of the aspen, which showed a recent aspen overstory mortality of 33%. The understory was composed of dense bracken fern (*Pteridium aquilinum*) and herbs/forbs (see Figure 3.2-B). We identified 10 aspen stems, 5 aspen snags, and 8 conifers (noble fir, Douglas-fir, and silver fir). The recruitment ratio (0.11) signaled a decreasing or unstable stand. When the aspen snags are included, the ratio more than doubles (0.25) but still remains 75% below what is needed for a stable stand. Only 2 sprouts were alive with second year growth. One (50%) was browsed and one (50%) was diseased for 2007. Neither sprout was ≥ 1 m in height. We found no ungulate or small mammal sign within this stand, even though it lies near a meadow that contains elk and deer sign.

Meadow Fringe

We classified 5 stands in our study area as Meadow Fringe. Three stands were subsequently classified as high elevation (>1500 m) and 2 stands as low elevation (<750 m).

High Elevation

The mean size for Meadow Fringe high elevation stands (*n*=3) was 0.64 ha (range: 0.006 – 0.06 m^2). All the stands occurred on the edge of a single wet meadow. Conifers had overtopped one stand which showed recent aspen overstory mortality of 40%. The other two stands lay in the open meadow and were not encroached upon by conifers (see Figure 3.3-C). These stands contained the largest and oldest aspen in our study area (see Figure 3.2-C). In the Meadow Fringe stand type, we identified a total 14 aspen stems, 1 aspen snag (3 logs), and 44 conifers (noble fir, grand fir, silver fir). These stands were decreasing or unstable (recruitment ratio = 0.44). When aspen snags and logs are included, the ratio decreased to 0.31. Nearly half of the recently recruited aspen stems were found growing within the branches of both live conifers and snags. Of the 104 sprouts in the stands, 26% were browsed, 31% were diseased and 42% were ≥ 1 m in height for 2007. We observed elk sign but no small mammal sign in the stands, which were also accessible to deer.

Low Elevation

Meadow Fringe low elevation stands (n = 2) had a mean area of 0.43 ha (range: 0.25 – 0.6 m^2). Both stands ringed the edge of a Douglas spiraea (*Spiraea douglassi*) bog. The aspen stems occurred between the bog's edge and the surrounding grand fir and Douglas-fir forest. Some aspen stems grew out in the bog where the soil was high enough to support them. We noted multiple stems that fell over due to lack of support from the wet soil out in the bog; there were no aspen logs in the dry portion of the stands. Additionally, we observed some of the fallen stems persisting and leafing-out for 2 years after having fallen over in the bog. Other overstory trees observed in the transition zone between the bog and the upland conifer forest included black cottonwood (*Populus trichocarpa*), black hawthorn (*Crataegus douglasii*), and Oregon crabapple (*Malus fusca*). The understory included many small trees and shrubs: willow (*Salix spp.*), red-osier dogwood (*Cornus sericea*), cascara, California wild-rose (*Rosa californica*), Oregon grape (*Mahonia aquifoliu*) in addition to herbs and forbs. We enumerated and measured 174 aspen stems, 5 aspen snags, and 83 conifers (Douglas-fir, grand fir). The stands had a recruitment ratio of 0.55 and were therefore listed as decreasing or unstable. Of the 296 aspen sprouts, 22% were browsed, 59% were diseased, and 20% were ≥ 1 m in height in 2007. These stands lie below the snow line for most of the winter, in an area considered an elk winter use area by the WNF and ODFW. Accordingly, we observed abundant elk sign in the area.

Lithic/Boulder

One stand occurred on a lithic site, which we classified as a boulder field type. At 1600 m in elevation, this was the highest stand in our study area. The stand was 0.4 ha in size and surrounded by boulders, making it free from conifer encroachment and large ungulate use across time (see Figure 3.3-D). However, the stand showed signs of heavy snow pack. Stems grew horizontally along the ground and boulders for 2-3m before growing upward. Some stems were bent downward from snow and continued to grow in that direction. The amount of soil available to the aspen for rooting may be limited in this substrate. Many older stems were found rotten or decaying in the understory, with new stems growing out of the bole section and new sprouts growing out of the root collar. We measured 307 aspen stems, no aspen snags, and no conifers. The stand had a recruitment ratio of 0.73 and was considered decreasing or unstable. Of the 154 sprouts, 32% were browsed, 19% were diseased, and 28% were $\geq$ 1 m in height in 2007. The herbivore in this case was the pika (*Ochotona princeps*), which had a colony in the boulder field. Because sprouts grew along the ground and in and around boulders, they were readily accessible to the pika.

Pasture Valley

Pasture Valley stands (n=3) occurred on the edge of one rancher's field at a low elevation (65 m). The stands averaged 0.01 m^2 (range: 0.004 – 0.015 m^2). We found no conifers in this stand type. Other deciduous trees growing in and around these stands included Oregon ash (*Fraxinus latifolia*) and black cottonwood. Understory included California wild-rose, grasses, and herbs/forbs. We enumerated

29 aspen stems, 7 aspen snags, and no conifers. This stand type had the lowest recruitment ratio in the study area at 0.03, and is considered to be decreasing and unstable. Of the 164 sprouts, 42% were browsed, 40% were diseased, and none were sprouts ≥ 1 m in height for 2007. A higher percentage of herbivory (27%) was from rabbits (*Sylvilagus* spp.) rather than from domestic livestock and wild ungulates (15%). Rabbits were able to browse aspen sprouts in rose thickets and other areas considered refugia from large ungulates. Browse from rabbits was only observed to occur < 35 cm in height. However, we observed sprouts > 35 cm that had been felled by rabbits and subsequently debarked or the tops consumed. Rabbit browse only occurred in the previous year's growth (2007) and did not occur by October for 2008. Livestock (cow, donkey, horse) were pastured in the field, giving them access to the aspen stands, which were also accessible to black-tailed deer.

Riparian Valley

Riparian Valley stands (*n*=3) were located along a farmer's field near the Calapooia River at 70 m in elevation. The stands averaged 0.17 ha in size (range: 0.02 – 0.41 ha). Two stands grew between an ash swale that was underwater most of the year and perennial and annual grass fields. The third stand grew along a fencerow in an open field. During our study, some of the aspen stems and sprouts were underwater for more than 5 winter months out of the year. Aspen that grew directly along the field edge were observed to have been mowed, trimmed, and singed by prescribed fire as part of agricultural practices. Sprouts that grew in the farmer's field had been damaged via mowing and herbicide use. One stand was narrow (35 m) but had extended 200 m along the ash swale. We enumerated 420 aspen stems, 31 aspen snags, and no conifers. The recruitment ratio for these stands was 1.2. This was the only stand type in our study area to have a recruitment ratio ≥ 1.0, indicating that the stand was stable or increasing in size. Of the 260 sprouts, none (0%) were browsed, 70% were diseased, and 42% were ≥ 1 m for 2007. The stands were accessible to deer, rabbits, and other small mammals. Domestic livestock (sheep) were grazed in the field, although 2 of the 3 stands had temporary fencing to keep the sheep from accessing the aspen.

DISCUSSION

Aspen stands and types have not been documented in this portion of the species range, nor has their conservation status been evaluated. Of the 16 stands we assessed in 8 areas, only one was previously mapped for western Oregon (Little, 1971). The stands in our study area differed from stands reported in the Intermountain West in two key ways. In general, the older aspen stems in our study area were 50-80 years younger than those reported in the Intermountain West (Hessl and Graumlich, 2002; Larsen and Ripple, 2003; Kaye *et al.*, 2005). Additionally, the aspen stands in western Oregon were small with a mean of 0.13 ha, far smaller than stands reported in other Western states (e.g., Colorado) making them difficult to compare to those in other studies. Small aspen stands tend to be uneven-aged (Betters and Woods, 1981) and may persist through small gaps in the canopy, with overstory recruitment across time (Kay, 1997a; Cumming *et al.*, 2000). Aspen in our study area were spatially correlated into 8 areas (stands ≥ 50m from each other) and suggests some areas may have contained a single larger stand. Additionally, aspen stands may have historically been more abundant in the Cascade Mountains and Willamette Valley. In the wilderness bordering our study area in the Central Oregon Cascades, a study found meadows decreased through conifer invasion during a recent period (1920 –1985) (Miller and Halpern, 1998). Similar to the Oregon white oak (*Quercus garryana*), aspen stands in the valley could have been diminished from the changes in human land use activity in the last century (Johannessen *et al.*, 1971).

The stressors identified for the 15 stands we assessed included: conifer encroachment, herbivory (large and small mammals), and disease (ASB). Similar to other studies (Kay and Bartos, 2000; Seager and Ripple, Chapter 2 this volume), we found disease alone was insufficient to suppress sprouts from growing into stems. Disease levels were highest in the Riparian Valley stand type (70% of all sprouts), and yet in the absence of herbivory, the sprouts were growing and recruiting into the overstory (recruitment ratio > 1.0). Similarly, conifer encroachment and herbivory may interact to produce a decrease in aspen sprout density and height (Seager and Ripple, Chapter 2 this volume). One additional herbivore found in the study area was the North American beaver (*Castor canadensis*). A stand was excluded from our study because of near complete overstory loss to the beaver. We noted felled aspen stems of varying sizes in the boulder field above the riparian area, showing extensive harvest by the beaver in a place large ungulates avoid. The beaver would need to be removed or excluded in order for the stand to recruit an overstory.

The recruitment ratios show that only one stand was stable or expanding (Table 3.1). However, the histograms of tree frequency and establishment decades indicates that 4 of the 6 stand types have recruited across time and seem to be persisting (Figure 3.2-A, C, D, F). Conversely, based on our survey, three stand types may be at risk of disappearing (Upland Aspen/Conifer, high elevation Meadow Fringe, and Pasture Valley, figure 3.2-B, C, and E respectively). We observed overstory mortality and decreased sprout density attributable to conifer encroachment in Meadow Fringe and Upland Aspen stands. We emphasize the need to consider overstory stressors in addition to those in the understory for stand persistence. We observed herbivory and disease suppressing sprout heights in many stands.

The stands origins are unknown. For the higher elevation stands, seeds could have dispersed across the crest of the Cascades from the east side. Once established, those stands could have dispersed seeds through wind or rivers to lower elevations. The valley stands could have originated as plantings from early settlers. The extent of one stand (> 200 m) suggests that a single planting by a settler along an ash swale is unlikely. The valley stands could have also originated from the Pleistocene Glacial Lake Missoula floods (c.a. 13,000 to 15,000 years before present). All valley aspen stands were less than 80 m in elevation, whereas the Missoula flood reached levels of 120 m in the Willamette Valley (Baldwin, 1959).

CONCLUSIONS

We reported on the trends that emerged from 6 different aspen stand types on an important tree species that has not been evaluated in this portion of its range.

Because of the paucity and small size of aspen stands in western Oregon, our observational study only included summary statistics and not inferential statistics. Nonetheless, the trends we observed may help managers and scientists and have high relevance for ecological restoration, because aspen represents such an ecologically important community type.

Results of this study show that aspen stands are rare and in decline in western Oregon. To preserve this species and habitat type, efforts should be made to protect and enhance aspen regeneration. Similar to what has been reported elsewhere in very small stands (< 0.1 ha), we found the regeneration periphery larger than the overstory core (Keyser *et al.*, 2005). This sprout area should be emphasized during restoration, with consideration of (1) conifer removal to decrease shading and increase sprout density, and (2) ungulate exclusion to lower herbivory and increase sprout height and recruitment (Bartos, 2001; Seager and Ripple, Chapter 2 this volume). In most stands, we found current sprouts were not recruiting into the overstory. Until that is remedied, we caution against cutting the aspen overstory to increase sprout density. Studies in the Oregon Cascades and Sierra Nevada found that overstory or ground disturbance was not necessary for successful aspen regeneration, only conifer removal and ungulate protection (Jones *et al.*, 2005 ; Seager and Ripple, Chapter 2 this volume). For the persistence of the overstory and continued sprout production, the mature aspen stems should be released from conifers that overtopped them. This would assure stand persistence until current sprouts recruit into the overstory. Aspen is a highly valued species in Oregon and the western US. Understanding aspen on the fringe of its range may help the persistence of the species in the face of climate change. A more thorough inventory and genetic analysis would help researchers and managers to understand the extent and origin of the species in this region.

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LITERATURE CITED

Applequist, M.B., 1958. A simple pith locator for use with off-center increment cores. J For 56, 141.

Bailey, J.K., Whitham, T.G., 2002. Interactions among Fire, Aspen, and Elk Affect Insect Diversity: Reversal of a Community Response. Ecology 83, 1701-1712.

Baker, W.L., Munroe, J.A., Hessl, A.E., 1997. The effects of elk on aspen in the winter range in Rocky Mountain National Park. Ecography 20, 155-165.

Baldwin, E.M., 1959. The Geology of Oregon. Edwards Brothers, Ann Arbor, Michigan, 136.

Bartos, D.L., 2001. Landscape dynamics of aspen and conifer forests.

Betters, D.R., Woods, R.F., 1981. Uneven-Aged Stand Structure and Growth of Rocky Mountain Aspen. J For 79, 673-676.

Blenis, P.V., 2007. Impact of simulated aspen shoot blight on trembling aspen. Can J For Res 37, 719-725.

Boyd, R., 1986. Strategies of Indian burning in the Willamette Valley. Canadian Journal of Anthropology 5, 65–86.

Crites, S., Dale, M.R.T., 1998. Diversity and abundance of bryophytes, lichens and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. Can J Bot 76, 641–651.

Cumming, S.G., Schmiegelow, F.K.A., Burton, P.J., 2000. Gap Dynamics in Boreal Aspen Stands: Is the Forest Older Than We Think? Ecol Appl 10, 744-759.

Debyle, N.V., 1985. Wildlife *in* Aspen: Ecology and management in the western United States. General Technical Report RM-119., Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, 135-152.

Dobkin, D.S., Rich, A.C., Pretare, J.A. and Pyle, W.H., 1995. Nest–site relationships among cavity-nesting birds of the riparian and snowpocket aspen woodlands in the northwestern Great Basin. Condor 97, 694–707.

Fisher, J.T., Wilkinson, L., 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mammal Rev 35, 51-81.

Flack, D.J.A., 1976. Bird populations of aspen forests in western North America. Ornithol Monogr 19, 1-97.

Griffis-Kyle, K.L., Beier, P., 2003. Small isolated aspen stands enrich bird communities in southwestern ponderosa pine forests. Biol Conserv 110, 375-385.

Hessl, A.E., Graumlich, L.J., 2002. Interactive effects of human activities, herbivory and fire on quaking aspen (*Populus tremuloides*) age structures in western Wyoming. J Biogeogr 29, 889-902.

Hinds, T.E., 1985. Diseases. Pages 87–114 in N. V. DeByle and R. P. Winokur, editors. Aspen: ecology and management in the western United States. USDA General Technical Report RM-119.

Johannessen, C.L., Davenport, W.A., Millet, A., McWilliams, S., 1971. The Vegetation of the Willamette Valley. Annals of the Association of American Geographers 61, 286-302.

Jones, B.E., Rickman, T.H., Vazquez, A., Sado, Y., Tate, K.W., 2005. Removal of encroaching conifers to regenerate degraded aspen stands in the Sierra Nevada. Restor Ecol 13, 373-379.

Kay, C.E., 1985. Aspen Reproduction in the Yellowstone Park - Jackson Hole Area and its Relationship to the Natural Regulation of Ungulates. in Workman, G.W. (ed.), Western Elk Management: A Symposium, Utah State University, Logan.

Kay, C.E., 1997. The condition and trend of aspen in Kootenay and Yoho National Parks: implications for ecological integrity. Canadian Field Naturalist 111, 607–616.

Kay, C.E., Bartos, D.L., 2000. Ungulate herbivory on Utah aspen: Assessment of long-term exclosures. J Range Manage 53, 145-153.

Kaye, M.W., Binkley, D., Stohlgren, T.J., 2005. Effects of Conifers and Elk Browsing on Quaking Aspen Forests in the Central Rocky Mountains, USA. Ecol Appl 15, 1284-1295.

Keyser, T.L., Smith, F.W., Shepperd, W.D., 2005. Trembling aspen response to a mixed-severity wildfire in the Black Hills, South Dakota, USA. Can J For Res 35, 2679-2684.

Kulakowski, D., Veblen, T.T., Drinkwater, S., 2004. The Persistence of Quaking Aspen (Populus Tremuloides) in the Grand Mesa Area, Colorado. Ecol Appl 14, 1603-1614.

Larsen, E.J., Ripple, W.J., 2003. Aspen age structure in the northern Yellowstone ecosystem: USA. For Ecol Manage 179, 469-482.

Little, E.L., Jr., 1971. Conifers and important hardwoods. Volume I. Atlas of United States trees. Forest Service Miscellaneous Publication Number 1146, Washington D.C., USA.

Miller, E.A., Halpern, C.B., 1998. Effects of environment and grazing disturbance on tree establishment in meadows of the central Cascade Range, Oregon, USA. Journal of Vegetation Science 9, 265-282.

Miller, R.E., Rose, J.A., 1995. Historic Expansion of Juniperus-Occidentalis (Western Juniper) in Southeastern Oregon. Great Basin Nat 55, 37-45.

Morrison, P.H., Swanson, F.J., 1990. Fire History and Pattern in a Cascade Range Landscape. Gen. Tech. Rep. PNW-GTR-254, USDA Forest Service, Portland, Oregon, 77 pp.

Mueggler, W.F., 1985. Vegetation associations. Pages 45–55 in N. V. DeByle and R. P. Winokur, editors. Aspen: ecology and management in the western United States. General Technical Report RM-119. United States Department of Agriculture Forest Service, Fort Collins, Colorado, USA.

Oaten, D.K., Larsen, K.W., 2009. Aspen Stands as Small Mammal "Hotspots" Within Dry Forest Ecosystems of British Columbia. Northwest Sci 82, 276-285.

ODFW, 2006. Aspen Woodlands, in Oregon Conservation Strategy. Oregon Deparment of Fish and Wildlife, Salem, Oregon. , 259-260.

Rakestraw, L., Rakestraw, M., 1991. History of the Willamette National Forest. United States Department of Agriculture, Willamette National Forest, Eugene, Oregon.

Ripple, W.J., Larsen, E.J., 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. Biol Conserv 95, 361-370.

Romme, W.H., Turner, M.G., Wallace, L.L., Walker, J.S., 1995. Aspen, Elk, and Fire in Northern Yellowstone Park. Ecology 76, 2097-2106.

Shepperd, W.D., Rogers, P.C., Burton, D., Bartos, D.L., 2006. Ecology, biodiversity, management, and restoration of aspen in the Sierra Nevada, General Technical Report RMRS-GTR-178. Rocky Mountain Research Station, USDA Forest Service, Fort Collins, Colorado, 122 p.

Shirley, D.M., Erickson, V., 2001. Aspen restoration in the Blue Mountains of Northeast Oregon. Pages 101-115 in Shepperd et al., compilers. Sustaining aspen in western landscapes: Symposium Proceedings. USDA Forest Service Rocky Mountain Research Station, RMRSP- 18, Grand Junction, Colorado.

Stokes, M.A., Smiley, T.L., 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago.

Sudworth, G.B., 1908. Forest trees of the Pacific slope. US Forest Service, Washington, D.C. 441 pp.

Wall, T.G., Miller, R.F., Svejcar, T.J., 2001. Juniper encroachment into aspen in the Northwest Great Basin. J Range Manage 54, 691-698.

White, C.A., Olmsted, C.E., Kay, C.E., 1998. Aspen, Elk, and Fire in the Rocky Mountain National Parks of North America. Wildl Soc Bull 26, 449-462.

Worrall, J.J., Egeland, L., Eager, T., Mask, R.A., Johnson, E.W., Kemp, P.A., Shepperd, W.D., 2008. Rapid mortality of Populus tremuloides in southwestern Colorado, USA. For Ecol Manage 255, 686-696.

Figure 3.1. Map of study area in western Oregon with aspen stand groups shown as dots.

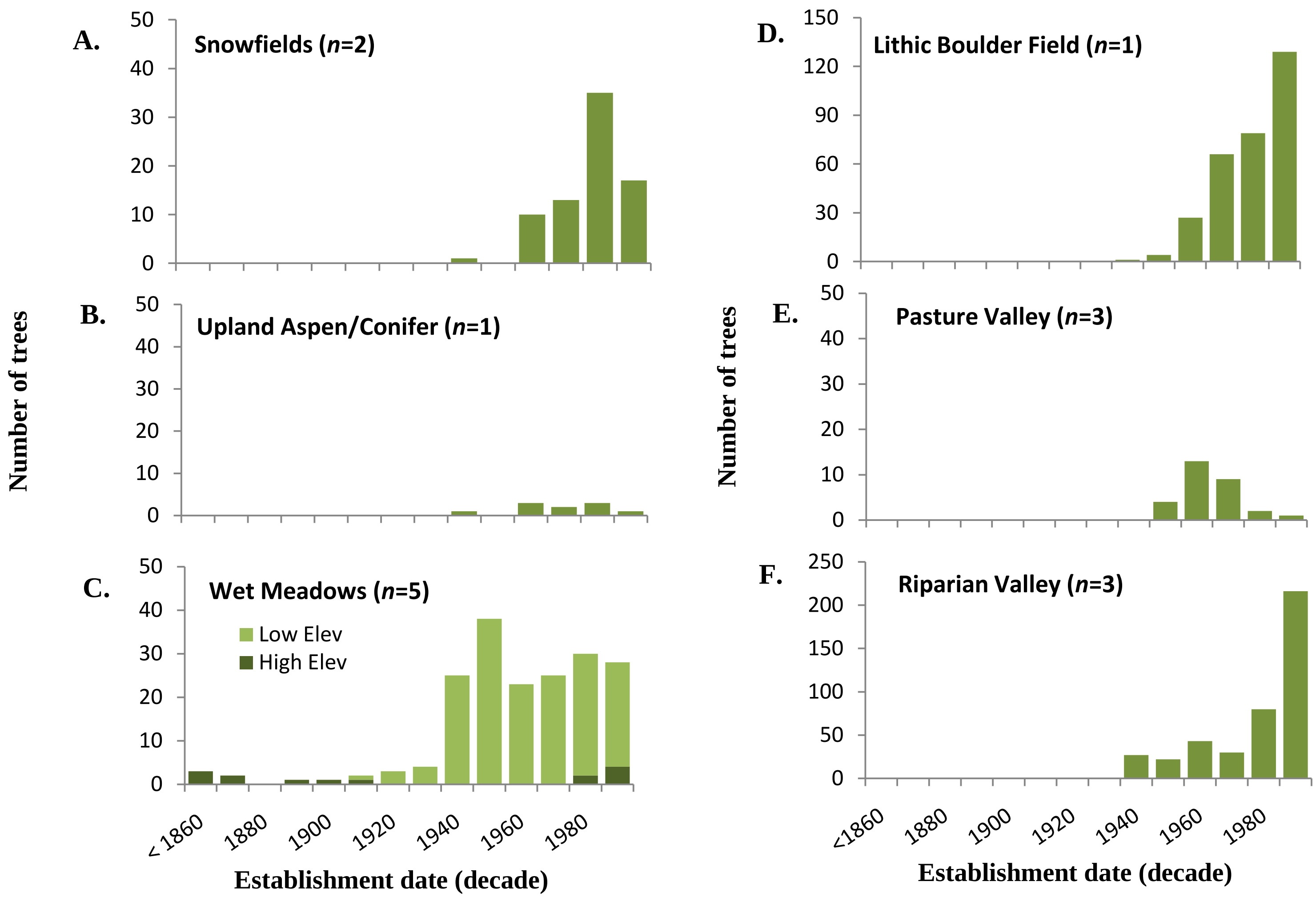

Figure 3.2. Aspen overstory trees by establishment date in each of the 6 stand types found in Western Oregon. *Note: Lithic/Boulder and Riparian Valley are on different scales.*

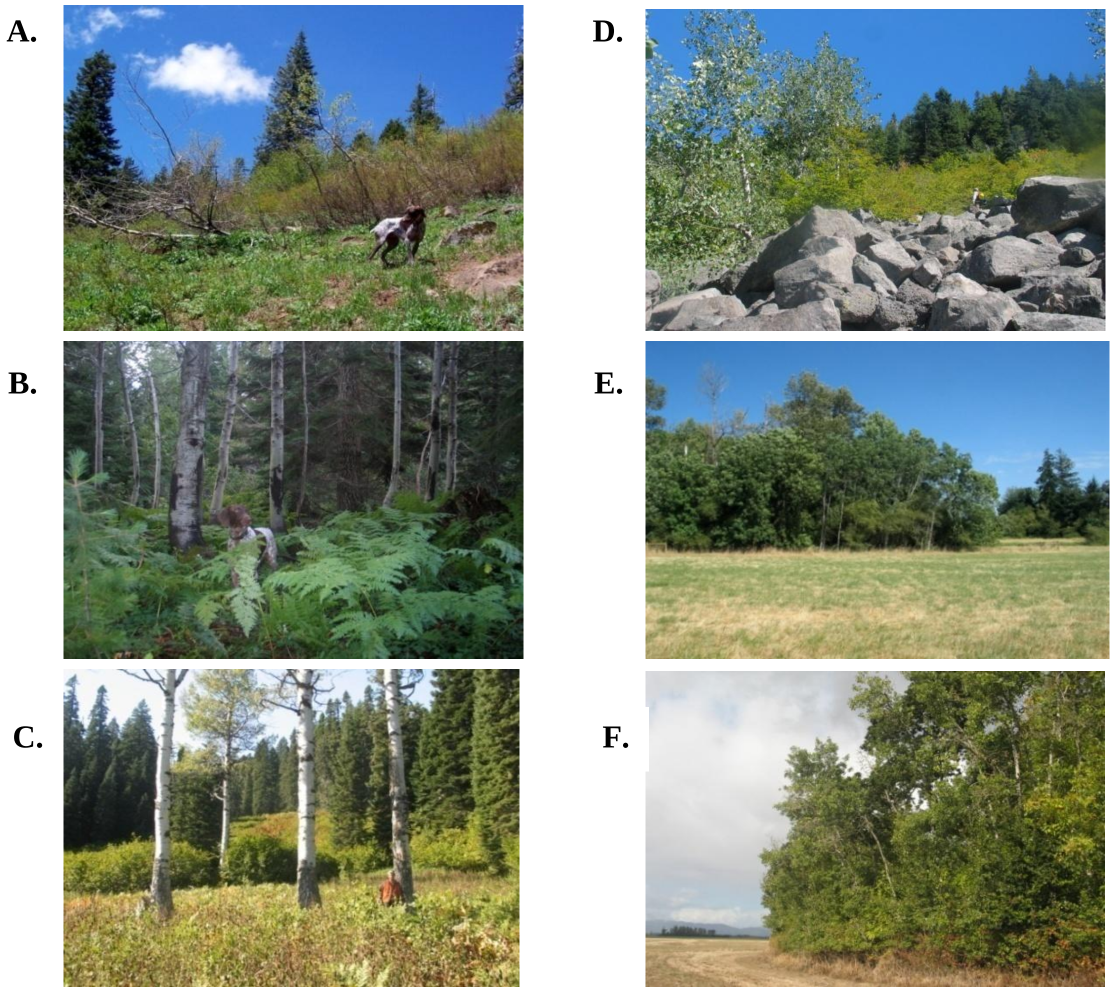

Figure 3.3. Six aspen stand types found in Western Oregon. A) Snowfield, B) Upland Aspen/Conifer, C) Meadow Fringe, D) Lithic/Boulder, E) Pasture (valley), and F) Riparian (valley).

Table 3.1 Overstory, understory, sprouts, and elevation for 6 aspen stand types found in western Oregon.

Aspen Stand Type		Total Stems	Recruitment Ratio[1]	Total Sprouts	Elevation mean	Stressors
Snowfield		76	0.39	193	1524 m	snowpack
Upland Aspen/Conifer		10	0.11	2	1132 m	disease, conifer
Meadow Fringe	*high elev.*	14	0.44	104	1377 m	disease, herbivory, conifer
	low elev.	174	0.55	296	730 m	disease, competition
Lithic/Boulder		307	0.73	154	1597 m	snowpack, herbivory
Pasture (valley)		29	0.03	164	66 m	herbivory, disease, farming
Riparian (valley)		420	1.2	260	69 m	disease, farming

[1]Recruitment ratio ≥ 1.0 is needed for a stand to be increasing or remaining stable (Kay 1985).

Table 3.2 Western Oregon Aspen Sprout Variables and Environmental Stressors

Variable	*Cascade Mountain Stand Types*					*Valley Stand Types*	
	Snowfield (*n*=193)	Upland Aspen/Conifer (*n*=2)	Meadow Fringe high elev (*n* = 104)	Meadow Fringe low elev (*n* = 296)	Lithic/ Boulder (*n*=154)	Pasture (*n*=164)	Riparian (*n*=260)
Sprout height (cm) 2007 mean (*standard deviation*)	77 (±46)	19 (±18)	92 (±7)	67 (±41)	74 (±70)	33 (±19)	97 (±49)
Annual growth of sprouts[1] (cm) 2008 mean (*standard deviation*)	29 (±19)	50 (±4)	21 (±12)	28 (±20)	17 (±14)	87 (±34)	28 (±25)
% Sprouts > 1m 2007	30%	0%	42%	20%	38%	0%	42%
% Browsed (ungulate) 2007	30%	50%	26%	22%	0%	15%	0%
% Browsed (small mammal) 2007	< 1%	0%	0%	0%	32%	27%	0%
% Diseased 2007	2%	50%	31%	59%	19%	40%	70%

[1]sprouts which were not browsed or diseased in 2008

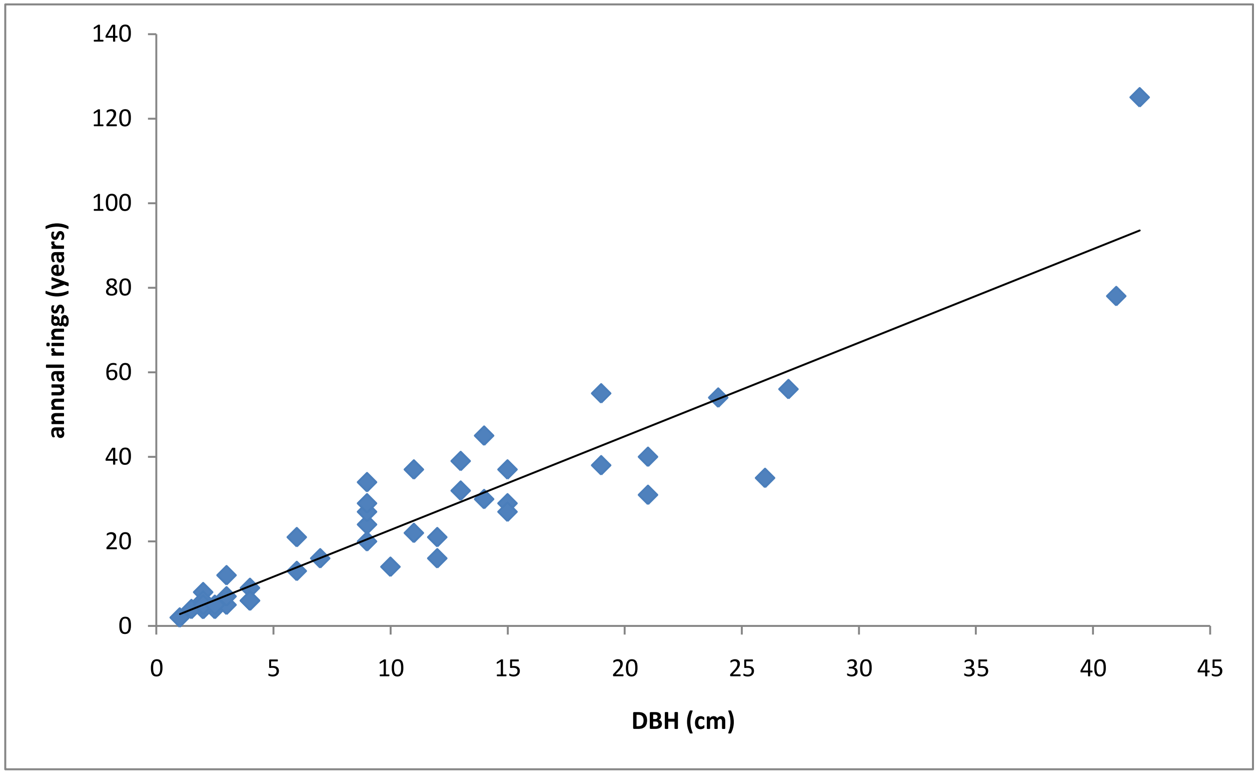

Figure 3.4. Aspen age diameter relationship using 34 tree cores and 17 saplings from the Oregon Cascade Mountains and the Willamette Valley ($r^2 = 0.86$, *p-value* < 0.001, *n* = 46).

Table 3.3 Herbivores found browsing on aspen sprouts in western Oregon

Common Name	Scientific name	Aspen Stand Type[1]
1. black-tailed deer	*Odocoileus hemionus columbianus*	SF, UA, MF, PV
2. Roosevelt elk	*Cervus canadensis roosevelti*	SF, UA, MF
3. North American beaver	*Castor canadensis*	RM[2]
4. Pika	*Ochotona princeps*	LB
5. Mountain beaver	*Aplodontia rufa*	SF
6. Eastern cottontail rabbit	*Sylvilagus floridanus*	PV, RV
7. Brush rabbit	*Sylvilagus bachmani*	PV, RV
8. Domestic sheep	*Ovis aries*	RV
9. Domestic cow, donkey, and horse	*Bos* spp.; *Equus asinus; Equus caballus*	PV

[1]Aspen stand types: Snowfield (SF), Upland Aspen/Conifer (UA), Meadow Fringe (MF), Lithic/Boulder (LB), Pasture valley (PV), Riparian valley (RV), Riparian mountain (RM).
[2]This stand type (RM) was excluded from our analysis due to overstory loss from beavers.

CHAPTER 4 – GENERAL CONCLUSIONS

In this thesis I assessed the current status of aspen stands in three Oregon landscapes and evaluated specific stressors on those stands in comparison to overstory recruitment across time. Aspen can be an indicator of ecological integrity, and can be evaluated over space and time (White *et al.*, 1998). In my complete enumeration of all aspen stems and coniferous trees in the selected aspen stand areas, I found aspen persisting but in decline in all three landscapes.

EAST CASCADES

On the eastern slope of the central Oregon Cascades, I found small aspen stands (≤ 0.6 ha) embedded in a dense conifer matrix. Conifer encroachment suppressed aspen sprout density, while herbivory suppressed aspen sprout height. Current aspen stands have persisted under ponderosa pine and lodgepole pine trees for over 200 years and possibly as long as the oldest pine (> 400 years). However, in the last century, active and passive fire suppression has allowed conifer encroachment in much higher densities (Agee, 1993). This infill and encroachment not only decreased available light and resources for mature aspen stems and aspen sprouts, but it also decreased available forage for domestic livestock and wild ungulates (Peek *et al.*, 2001) putting more pressure on the remaining aspen sprouts.

Surprisingly, aspen stands that experienced the most conifer encroachment were the stands most likely to have recently recruited aspen into the overstory. This ecological twist is played out by a powerful driver in the dry pine forests of the east side, the mountain pine beetle. The beetle-killed lodgepole pine released conifer pressure on the aspen overstory, allowing mature aspen stems to persist and aspen sprout density to increase. When the lodgepole snags fell across the next decade (Mitchell and Preisler, 1998) the ensuing jackstraw created an herbivore barrier that proved effective in allowing aspen sprouts to recruit into the overstory. Although ungulates do not overwinter in my study area, the jackstraw was found important for aspen sprout recruitment into the overstory. More than 75% of all recently recruited stems were behind jackstraw. This finding reinforces that managers should use caution in disturbing the aspen overstory (e.g., burning, cutting) until ungulate herbivory is controlled. Additionally, conifer removal efforts should consider that mature pines have persisted with aspen for hundreds of years.

Aspen ecosystems are critical wildlife habitat in the eastern Cascades dry forest systems (ODFW, 2006) and are prioritized as part of mixed conifer and dry pine forest restoration (Johnson and Franklin, 2009). The findings from this study provide valuable insight into the current status of aspen stands in those systems, and potential steps toward aspen ecosystem restoration.

WEST CASCADES AND WILLAMETTE VALLEY

On the western slope of the central Oregon Cascades, aspen stands are rare and in decline. These small stands (≤ 0.1 ha) occur as many distinct habitat types, and efforts should be made to protect and enhance these aspen ecosystems. Because the stands are small, emphasis should be on the regeneration periphery (Keyser *et al.*, 2005) where conifer encroachment and herbivory were found suppressing aspen sprouts and therefore overstory recruitment. On the Willamette Valley floor, a few aspen stands have persisted in a landscape of agriculture and livestock grazing. The valley stands should be considered the most at-risk because of their location. Until their genetic origin can be determined, I recommend these stands be treated as genetically isolated and different from eastern and western Cascade stands.

Aspen are outside of their expected range in western Oregon. They face unique environmental stressors, such as much higher amounts of precipitation than in the rest of their intermountain range. Herbivory affected aspen sprout heights and recruitment in some stands, and most likely interacted with disease in a landscape where moisture levels and vegetation competition are high. The stressors these stands face may help scientists better understand this species, and could provide insight into helping this important wildlife habitat persist in the face of climate change.

FUTURE RESEARCH

Aspen is an important wildlife habitat in the intermountain west. The need for research of the specific drivers of aspen stand persistence or decline for each geographic location in the region has been emphasized in part because of the diversity of landscapes where aspen occur (Kashian *et al.*, 2007). This thesis provides insight into three landscapes where aspen has not been previously studied. Future research should focus on stand vigor when released from conifer encroachment and herbivory (White *et al.*, 1998; Bartos, 2001). Decreasing these pressures on aspen stands can make them less susceptible to larger climactic patterns (Gitlin *et al.*, 2006).

Research shows that as climate shifts, the available climate profile for aspen in Oregon and the intermountain west will diminish rapidly over the next century (Rehfeldt *et al.*, 2009). This model did not include aspen in western Oregon in its current year (2000) profile, and therefore did not model this region into the future. Aspen in western Oregon may respond quite differently to climate change. The dramatic aspen decline noted in the Rockies found that stands in lower elevation and south-easterly slopes were more at-risk of decline (Worrall *et al.*, 2008). In combination with the climate change model for aspen (Rehfeldt *et al.*, 2009), this suggests that land managers should plan for aspen to persist in, and possibly move to, higher elevations. This thesis provides current stressor and aspen stand information that may help land managers in that planning.

Some research has suggested that phenology may be a key determinant in a tree species range (Chuine and Beaubien, 2001). I observed the aspen in the Willamette Valley and western Oregon had earlier leaf-out and later leaf-drop than those in the Cascade Mountains. The stands in the Cascades had varying phenology based on elevation and snow pack. Future research could include experiments with aspen sprouts from across western and eastern Oregon grown in identical situations (e.g., greenhouse) to test for determining factors of observed phenology. In addition, aspen sprouts from varying locations within the study area could be transplanted to other stand areas in an experiment to observe the phenology and response to environmental and biological stressors of transplanted sprouts.

In addition to the future research outlined in Chapters 2 and 3, the genetics and phenology of aspen in western Oregon may provide valuable insight into this species' persistence.

LITERATURE CITED

Agee, J.K., 1993. Fire Ecology of Pacific Northwest Forests, Island Press, Washington, DC (1993) 493 pp.

Bartos, D.L., 2001. Landscape dynamics of aspen and conifer forests.

Chuine, I., Beaubien, E.G., 2001. Phenology is a major determinant of tree species range. Ecol Lett 4, 500-510.

Gitlin, A.R., Sthultz, C.M., Bowker, M.A., Stumpf, S., Paxton, K.L., Kennedy, K., Muñoz, A., Bailey, J.K., Whitham, T.G., 2006. Mortality Gradients within and among Dominant Plant Populations as Barometers of Ecosystem Change During Extreme Drought. Conserv Biol 20, 1477-1486.

Johnson, N.K., Franklin, J.F., 2009. Restoration of Federal Forests in the Pacific Northwest: Strategies and Management Implications. Special report to Senator Wyden and Congressman DeFazio., 120 pp.

Kashian, D.M., Romme, W.H., Regan, C.M., 2007. Reconciling Divergent Interpretations of Quaking Aspen Decline on the Northern Colorado Front Range. Ecol Appl 17, 1296-1311.

Keyser, T.L., Smith, F.W., Shepperd, W.D., 2005. Trembling aspen response to a mixed-severity wildfire in the Black Hills, South Dakota, USA. Can J For Res 35, 2679-2684.

Mitchell, R.G., Preisler, H.K., 1998. Fall Rate of Lodgepole Pine Killed by the Mountain Pine Beetle in Central Oregon. West J Appl For 13, 23-26.

ODFW, 2006. Aspen Woodlands, in Oregon Conservation Strategy. Oregon Department of Fish and Wildlife, Salem, Oregon. , 259-260.

Peek, J.M., Korol, J.J., Gay, D., Hershey, T., 2001. Overstory-understory biomass changes over a 35-year period in southcentral Oregon. For Ecol Manage 150, 267-277.

Rehfeldt, G.E., Ferguson, D.E., Crookston, N.L., 2009. Aspen, climate, and sudden decline in western USA. For Ecol Manage 258, 2353-2364.

White, C.A., Olmsted, C.E., Kay, C.E., 1998. Aspen, Elk, and Fire in the Rocky Mountain National Parks of North America. Wildl Soc Bull 26, 449-462.

Worrall, J.J., Egeland, L., Eager, T., Mask, R.A., Johnson, E.W., Kemp, P.A., Shepperd, W.D., 2008. Rapid mortality of Populus tremuloides in southwestern Colorado, USA. For Ecol Manage 255, 686-696.

ACCUMULATIVE LITERATURE CITED

Abella, S.R., 2005. Environmental and vegetational gradients on an Arizona ponderosa pine landscape: implications for ecological restoration. Doctoral dissertation, Northern Arizona University, Flagstaff, AZ. 184 pp.

Agee, J.K., 1993. Fire Ecology of Pacific Northwest Forests, Island Press, Washington, DC (1993) 493 pp.

Applequist, M.B., 1958. A simple pith locator for use with off-center increment cores. J For 56, 141.

Bailey, J.K., Whitham, T.G., 2002. Interactions among Fire, Aspen, and Elk Affect Insect Diversity: Reversal of a Community Response. Ecology 83, 1701-1712.

Bailey, V., 1936. *The mammals and life zones of Oregon.* N Am Fauna 55, 416 pp.

Baker, W.L., Munroe, J.A., Hessl, A.E., 1997. The effects of elk on aspen in the winter range in Rocky Mountain National Park. Ecography 20, 155-165.

Baldwin, E.M., 1959. The Geology of Oregon. Edwards Brothers, Ann Arbor, Michigan, 136.

Bartos, D.L., 2001. Landscape dynamics of aspen and conifer forests.

Bates, J.D., Miller, R.F., Davies, K.W., 2006. Restoration of Quaking Aspen Woodlands Invaded by Western Juniper. Rangeland Ecology and Management 59, 88-97.

Betters, D.R., Woods, R.F., 1981. Uneven-Aged Stand Structure and Growth of Rocky Mountain Aspen. J For 79, 673-676.

Blenis, P.V., 2007. Impact of simulated aspen shoot blight on trembling aspen. Can J For Res 37, 719-725.

Bork, J., 1985. Fire history in three vegetation types on the east side of the Oregon Cascades. Ph.D. Dissertation. Oregon State University, Corvallis, OR.

Boyd, R., 1986. Strategies of Indian burning in the Willamette Valley. Canadian Journal of Anthropology 5, 65–86.

Brown, K., Hansen, A., Keane, R., Graumlich, L., 2006. Complex interactions shaping aspen dynamics in the Greater Yellowstone Ecosystem. Landsc Ecol 21, 933-951.

Carlson, D.W., Groot, A., 1997. Microclimate of clear-cut, forest interior, and small openings in trembling aspen forest. Agricultural and Forest Meteorology 87, 313-329.

Chantal, M.d., Granström, A., 2007. Aggregations of dead wood after wildfire act as browsing refugia for seedlings of Populus tremula and Salix caprea. For Ecol Manage 250, 3-8.

Chong, G.W., Simonson, S.E., Stohlgren, T.J., Kalkhan, M.A., 2001. Biodiversity: aspen stands have the lead, but will nonnative species

take over? Pages 261–271 in W. D. Shepperd, D. Binkley, D. L. Bartos, T. J. Thomas, and L. G. Eskew, compilers. Sustaining aspen in western landscapes: Symposium Proceedings. USDA Forest Service Rocky Mountain Research Station, RMRS-P-18, Grand Junction, Colorado.

Chuine, I., Beaubien, E.G., 2001. Phenology is a major determinant of tree species range. Ecol Lett 4, 500-510.

Crites, S., Dale, M.R.T., 1998. Diversity and abundance of bryophytes, lichens and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. Can J Bot 76, 641–651.

Cumming, S.G., Schmiegelow, F.K.A., Burton, P.J., 2000. Gap Dynamics in Boreal Aspen Stands: Is the Forest Older Than We Think? Ecol Appl 10, 744-759.

Debyle, N.V., 1985a. Animal Impacts *in* Aspen: Ecology and management in the western United States. General Technical Report RM-119., Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, 115-123.

Debyle, N.V., 1985b. Wildlife *in* Aspen: Ecology and management in the western United States. General Technical Report RM-119., Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, 135-152.

Debyle, N.V., Winokur, R.P., 1985. Aspen: Ecology and management in the western United States. General Technical Report RM-119., Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, 283p.

Di Orio, A.P., Callas, R., Schaefer, R.J., 2005. Forty-eight year decline and fragmentation of aspen (Populus tremuloides) in the South Warner Mountains of California. For Ecol Manage 206, 307-313.

Dobkin, D.S., Rich, A.C., Pretare, J.A. and Pyle, W.H., 1995. Nest–site relationships among cavity-nesting birds of the riparian and snowpocket aspen woodlands in the northwestern Great Basin. Condor 97, 694–707.

Fisher, J.T., Wilkinson, L., 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mammal Rev 35, 51-81.

Flack, D.J.A., 1976. Bird populations of aspen forests in western North America. Ornithol Monogr 19, 1-97.

Forester, J.D., Anderson, D.P., Turner, M.G., 2007. Do high-density patches of coarse wood and regenerating saplings create browsing refugia for aspen (Populus tremuloides Michx.) in Yellowstone National Park (USA)? For Ecol Manage 253, 211-219.

Gitlin, A.R., Sthultz, C.M., Bowker, M.A., Stumpf, S., Paxton, K.L., Kennedy, K., Muñoz, A., Bailey, J.K., Whitham, T.G., 2006. Mortality Gradients within and among Dominant Plant Populations as Barometers of Ecosystem Change During Extreme Drought. Conserv Biol 20, 1477-1486.

Griffis-Kyle, K.L., Beier, P., 2003. Small isolated aspen stands enrich bird communities in southwestern ponderosa pine forests. Biol Conserv 110, 375-385.

Harper, J.A., 1985. Ecology and management of Roosevelt elk in Oregon. Oregon Department of Fish and Wildlife, Portland, Oregon., 70 pp.

Hessburg, P.F., Agee, J.K., 2003. An environmental narrative of Inland Northwest United States forests, 1800-2000. For Ecol Manage 178, 23-59.

Hessl, A.E., Graumlich, L.J., 2002. Interactive effects of human activities, herbivory and fire on quaking aspen (*Populus tremuloides*) age structures in western Wyoming. J Biogeogr 29, 889-902.

Hinds, T.E., 1985. Diseases. Pages 87–114 in N. V. DeByle and R. P. Winokur, editors. Aspen: ecology and management in the western United States. USDA General Technical Report RM-119.

Hogg, E.H.T.e.d., Brandt, J.P., Michaelian, M., 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Can J For Res 38, 1373-1384.

Johannessen, C.L., Davenport, W.A., Millet, A., McWilliams, S., 1971. The Vegetation of the Willamette Valley. Annals of the Association of American Geographers 61, 286-302.

Johnson, N.K., Franklin, J.F., 2009. Restoration of Federal Forests in the Pacific Northwest: Strategies and Management Implications. Special report to Senator Wyden and Congressman DeFazio., 120 pp.

Jones, B.E., Rickman, T.H., Vazquez, A., Sado, Y., Tate, K.W., 2005. Removal of encroaching conifers to regenerate degraded aspen stands in the Sierra Nevada. Restor Ecol 13, 373-379.

Kashian, D.M., Romme, W.H., Regan, C.M., 2007. Reconciling Divergent Interpretations of Quaking Aspen Decline on the Northern Colorado Front Range. Ecol Appl 17, 1296-1311.

Kay, C.E., 1985. Aspen Reproduction in the Yellowstone Park - Jackson Hole Area and its Relationship to the Natural Regulation of Ungulates. in Workman, G.W. (ed.), Western Elk Management: A Symposium, Utah State University, Logan.

Kay, C.E., 1997a. The condition and trend of aspen in Kootenay and Yoho National Parks: implications for ecological integrity. Canadian Field Naturalist 111, 607–616.

Kay, C.E., 1997b. Is Aspen Doomed? J For 95, 4-11.

Kay, C.E., 2001. Long-term aspen exclosures in Yellowstone ecosystem. Pages 225–240 in W. D. Shepperd, D. Binkley, D. L. Bartos, and T. J. Stohlgren, compilers. Sustaining aspen in western landscapes: symposium proceedings, 13– 15 June 2000, Grand Junction, Colorado. USDA Forest Service, RMRS-P-18. Fort Collins, Colorado, USA.

Kay, C.E., Bartos, D.L., 2000. Ungulate herbivory on Utah aspen: Assessment of long-term exclosures. J Range Manage 53, 145-153.

Kaye, M., Stohlgren, T., Binkley, D., 2003. Aspen structure and variability in Rocky Mountain National Park, Colorado, USA. Landsc Ecol 18, 591-603.

Kaye, M.W., Binkley, D., Stohlgren, T.J., 2005. Effects of Conifers and Elk Browsing on Quaking Aspen Forests in the Central Rocky Mountains, USA. Ecol Appl 15, 1284-1295.

Keyser, T.L., Smith, F.W., Shepperd, W.D., 2005. Trembling aspen response to a mixed-severity wildfire in the Black Hills, South Dakota, USA. Can J For Res 35, 2679-2684.

Kota, A.M., 2005. Fences and on-site forest materials as ungulate barriers to promote aspen persistence in the Black Hills. M.S. thesis, Utah State University, Logan, UT, 74 pages.

Kulakowski, D., Veblen, T.T., Drinkwater, S., 2004. The Persistence of Quaking Aspen (Populus Tremuloides) in the Grand Mesa Area, Colorado. Ecol Appl 14, 1603-1614.

Larsen, E.J., Ripple, W.J., 2003. Aspen age structure in the northern Yellowstone ecosystem: USA. For Ecol Manage 179, 469-482.

Larsson, S., Oren, R., Waring, R.H., Barrett, J.W., 1983. Attacks of Mountain Pine Beetle as Related to Tree Vigor of Ponderosa Pine. For Sci 29, 395-402.

Little, E.L., Jr., 1971. Conifers and important hardwoods. Volume I. Atlas of United States trees. Forest Service Miscellaneous Publication Number 1146, Washington D.C., USA.

Milchunas, D.G., Noy-Meir, I., 2002. Grazing refuges, external avoidance of herbivory and plant diversity. Oikos 99, 113-130.

Miller, E.A., Halpern, C.B., 1998. Effects of environment and grazing disturbance on tree establishment in meadows of the central Cascade Range, Oregon, USA. Journal of Vegetation Science 9, 265-282.

Miller, R.E., Rose, J.A., 1995. Historic Expansion of Juniperus-Occidentalis (Western Juniper) in Southeastern Oregon. Great Basin Nat 55, 37-45.

Mitchell, R.G., Preisler, H.K., 1998. Fall Rate of Lodgepole Pine Killed by the Mountain Pine Beetle in Central Oregon. West J Appl For 13, 23-26.

Morrison, P.H., Swanson, F.J., 1990. Fire History and Pattern in a Cascade Range Landscape. Gen. Tech. Rep. PNW-GTR-254, USDA Forest Service, Portland, Oregon, 77 pp.

Mueggler, W.F., 1985. Vegetation associations. Pages 45–55 in N. V. DeByle and R. P. Winokur, editors. Aspen: ecology and management in the western United States. General Technical Report RM-119. United States Department of Agriculture Forest Service, Fort Collins, Colorado, USA.

Oaten, D.K., Larsen, K.W., 2009. Aspen Stands as Small Mammal "Hotspots" Within Dry Forest Ecosystems of British Columbia. Northwest Sci 82, 276-285.

ODFW, 2003a. Oregon's Elk Management Plan. Oregon Department of Fish and Wildlife, Portland, Oregon., 63 pp.

ODFW, 2003b. Oregon's Mule Deer Management Plan. Oregon Department of Fish and Wildlife, Portland, Oregon., 29 pp.

ODFW, 2006. Aspen Woodlands, in Oregon Conservation Strategy. Oregon Department of Fish and Wildlife, Salem, Oregon. , 259-260.

Peek, J.M., Dennis, B., Hershey, T., 2002. Predicting Population Trends of Mule Deer. The Journal of Wildlife Management 66, 729-736.

Peek, J.M., Korol, J.J., Gay, D., Hershey, T., 2001. Overstory-understory biomass changes over a 35-year period in southcentral Oregon. For Ecol Manage 150, 267-277.

Pinherio, J.C., Bates, D.M., 2000. Mixed-effect Models in S and S-PLUS. New York: Springer.

Rakestraw, L., Rakestraw, M., 1991. History of the Willamette National Forest. United States Department of Agriculture, Willamette National Forest, Eugene, Oregon.

Rehfeldt, G.E., Ferguson, D.E., Crookston, N.L., 2009. Aspen, climate, and sudden decline in western USA. For Ecol Manage 258, 2353-2364.

Reynolds, H.G., 1969. Aspen grove use by deer, elk, and cattle in southwestern coniferous forests. United States Department of Agriculture Forest Service, Research Paper RM-138.

Ripple, W.J., Beschta, R.L., 2005. Refugia from browsing as reference sites for restoration planning. West N Am Nat 65, 269-273.

Ripple, W.J., Beschta, R.L., 2007. Restoring Yellowstone's aspen with wolves. Biol Conserv 138, 514-519.

Ripple, W.J., Larsen, E.J., 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. Biol Conserv 95, 361-370.

Ripple, W.J., Larsen, E.J., 2001. The Role of Postfire Coarse Woody Debris in Aspen Regeneration. West J Appl For 16, 61-64.

Romme, W.H., Turner, M.G., Tuskan, G.A., Reed, R.A., 2005. Establishment, Persistence, and Growth of Aspen (Populus tremuloides) Seedlings in Yellowstone National Park. Ecology 86, 404-418.

Romme, W.H., Turner, M.G., Wallace, L.L., Walker, J.S., 1995. Aspen, Elk, and Fire in Northern Yellowstone Park. Ecology 76, 2097-2106.

Rumble, M.A., Pella, T., Sharps, J.C., Carter, A.V., Parrish, B.J., 1996. Effects of logging slash on aspen regeneration in grazed clearcuts. The Prairie Naturalist 28, 199–209.

Salwasser, H., 1979. The ecology and management of the Devil’s Garden Interstate Deer Herd and its range. Ph.D. Dissertation, University of California (Berkeley).

Schier, G.A., Jones, J.R., Winokur, R.P., 1985. Vegetative regeneration. In: N. V. DeByle and R. P. Winokur, eds. Aspen: ecology and management in the western

United States. USDA, For. Serv. Rocky Mountain Forest and Range Experiment Station. Fort Collins, CO. Gen. Tech. Rep RM-119: 20–33.

Shepperd, W.D., Battaglia, M.A., 2002. Ecology, siliviculture, and management of Black Hills ponderosa pine. Gen. Tech. Rep. RMRS-GTR-97. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 112 p.

Shepperd, W.D., Rogers, P.C., Burton, D., Bartos, D.L., 2006. Ecology, biodiversity, management, and restoration of aspen in the Sierra Nevada, General Technical Report RMRS-GTR-178. Rocky Mountain Research Station, USDA Forest Service, Fort Collins, Colorado, 122 p.

Shirley, D.M., Erickson, V., 2001. Aspen restoration in the Blue Mountains of Northeast Oregon. Pages 101-115 in Shepperd et al., compilers. Sustaining aspen in western landscapes: Symposium Proceedings. USDA Forest Service Rocky Mountain Research Station, RMRSP- 18, Grand Junction, Colorado.

Stokes, M.A., Smiley, T.L., 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago.

Sudworth, G.B., 1908. Forest trees of the Pacific slope. US Forest Service, Washington, D.C. 441 pp.

Thilenius, J.F., 1972. Classification of deer habitat in the ponderosa pine forest of the Black Hills, South Dakota. Res. Pap. RM-91. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, 28 p.

Verts, B.J., Carraway, L.N., 1998. Land Mammals of Oregon. University of California Press, Berkeley, CA, 668.

Wall, T.G., Miller, R.F., Svejcar, T.J., 2001. Juniper encroachment into aspen in the Northwest Great Basin. J Range Manage 54, 691-698.

White, C.A., Olmsted, C.E., Kay, C.E., 1998. Aspen, Elk, and Fire in the Rocky Mountain National Parks of North America. Wildl Soc Bull 26, 449-462.

Williams, D.W., Liebhold, A.M., 2002. Climate change and the outbreak ranges of two North American bark beetles. Agric For Entomol 4, 87-99.

Worrall, J.J., Egeland, L., Eager, T., Mask, R.A., Johnson, E.W., Kemp, P.A., Shepperd, W.D., 2008. Rapid mortality of Populus tremuloides in southwestern Colorado, USA. For Ecol Manage 255, 686-696.

Worrell, R., 1995. European aspen (Populus tremula L.): a review with particular reference to Scotland I. Distribution, ecology and genetic variation. Forestry 68, 93-105.

Zalunardo, R.A., 1965. The Seasonal Distribution of a Migratory Mule Deer Herd. The Journal of Wildlife Management 29, 345-351.